



Status signalling, metabolic rate and body mass in the siskin: the cost of being a subordinate

JUAN CARLOS SENAR*, VICENTE POLO†, FRANCESC URIBE* & MONTSE CAMERINO*

*Museu de Zoologia de Barcelona

†Museo Nacional de Ciencias Naturales

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The higher metabolic rate of dominant individuals, found in different species, has been interpreted as the cost that prevents subordinates from cheating by adopting large badges of status. However, an alternative prediction for status-signalling species, in which subordinates may recognize dominants, is that subordinates have the higher metabolic rate because of the greater stress of locating and actively avoiding aggressive interactions with them. In this study, the size of the black bib of the siskin, *Carduelis spinus*, which is a badge of dominance, was negatively correlated with metabolic rate in daylight, even when controlling for the bird's activity level in the respirometer chamber and its body mass. The size of the black bib, however, was not correlated with metabolic rate in darkness. This suggests that the difference between dominance classes is not related to intrinsic physiological differences, but that subordinates are more susceptible to stressful conditions. When controlling for metabolic rate, a positive correlation appeared between dominance status and body mass. This stresses the importance of knowing the effects of social status on energy requirements for understanding the relationship between body mass and dominance. We conclude that maintaining a high social status may be more stressful to subordinates than to dominant birds.

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Dominance provides many advantages, from preferential access to resources, the best habitats or safer locations, to higher survival or maturing at a younger age (reviewed in Huntingford & Turner 1987; Senar 1994; Piper 1997). On the other hand, dominant individuals often have a higher metabolic rate than subordinates, either during the day (Roskaft et al. 1986; Hogstad 1987; Reinertsen & Hogstad 1994; Metcalfe et al. 1995) or at night (Bryant & Newton 1994), which has been interpreted as a cost to dominance (but see Metcalfe et al. 1995 for a different interpretation on salmonids). Thus, the benefits of a high social status, in relation to improved resource access, can be diminished by more frequent agonistic encounters and interactions that increase the metabolic rate (Roskaft et al. 1986). This physiological cost could help to explain the evolutionary stability of social systems (e.g. Hogstad 1987; Johnstone & Norris 1993). That dominants can obtain more energy than subordinates (Senar 1994; Piper 1997) and have higher body mass (e.g. Baker & Fox 1978; Lundberg 1985; Piper & Wiley 1990) additionally sup-

ports the view that dominants have a higher metabolic rate than subordinates.

There is no evolutionary reason to predict a higher metabolic rate in dominant individuals however. In several species subordinates weigh more than dominants (e.g. Ekman & Lilliendahl 1992; Witter & Swaddle 1995; Hake 1996), which could entail a higher metabolic rate. Subordinates forage under higher predation risks than dominants in natural habitats (Ekman & Askenmo 1984; Ekman 1987; Hogstad 1988b) and this has been replicated in experiments where they had to fly further to get food (Hogstad 1988a; Koivula et al. 1994; Slotow & Rothstein 1995). After a predation attack, subordinates resume foraging earlier (De Laet 1985; Hegner 1985; Hogstad 1988a) and are more vigilant both for predators and dominant flock companions (Knight & Knight 1986; Waite 1987a, b). Subordinates receive a disproportionate amount of aggression (Keys & Rothstein 1991), and have to wait their turn when foraging on limited resources, while dominants just arrive and take them (Craig et al. 1982; Pöysä 1988; Ramenofsky et al. 1992). Dominants feed without interruptions while subordinates are always attentive to the behaviour and location of dominants, constantly moving around them trying to get some food. All this probably entails more stress (Belthoff et al. 1994)

Correspondence: J. C. Senar, Museu de Zoologia, Ap. Correu 593, 08080 Barcelona, Spain (email: jcsenar@intercom.es). V. Polo is at the Departamento Ecología Evolutiva, Museo Nacional Ciencias Naturales, J. Gutiérrez Abascal 2, 28006 Madrid, Spain.

and, in turn, a higher metabolic rate for subordinates. This could especially be the case for stable social groups, since subordinates recognize dominant flock members, while dominants, being recognized as such, may just enjoy their higher social status (see Cristol 1995, for a similar reasoning).

Status-signalling species, in which plumage colour patches are used to signal social dominance (Whitfield 1987; Senar 1999), may be highly relevant to this topic. According to the status-signalling hypothesis, superior fighters (i.e. dominants) benefit from these badges of status because they engage in fewer aggressive contests to maintain dominance status or priority of access to resources, and subordinates benefit by avoiding interactions with superior individuals (Rohwer & Rohwer 1978; Whitfield 1987). By using badges of status, subordinate birds are able to recognize the relative dominance ability of other individuals without requiring overt aggression (Senar & Camerino 1998). This, however, may have a cost. Because of the status signals, individuals in these species may behave continuously as in socially stable groups, so that, as reasoned above, subordinates may have to be continuously attentive to the badges of status of flock companions, while dominants may trust their own status. The classic reasoning to explain a higher metabolic rate in dominants is that these individuals are often involved in aggressive encounters to enforce their dominance (Roskaft et al. 1986; Hogstad 1987). An alternative prediction for status-signalling species, in which subordinates may recognize dominants (Senar & Camerino 1998), is that subordinates have a higher metabolic rate because of the greater stress of locating and actively avoiding aggressive interactions with dominants, which in turn, in addition to having the 'standard' advantages of dominance, are avoided by subordinates without having to enforce their higher status by aggression.

Our aim was to explore the relationship between badges of status and metabolic rate. A previous study (Roskaft et al. 1986) tested for this relationship indirectly, but unfortunately plumage variability was strongly related to sex and age differences, so that variation in metabolic rate could have been related more to sex/age than to dominance. Here we use data on the siskin, *Carduelis spinus*, for which we have already shown that the size of the black bib works as a signal of social status independently of the sex and age of the birds (Senar et al. 1993; Senar 1999).

METHODS

We trapped 24 male siskins between December 1996 and February 1997 in Barcelona, Spain, and kept them in individual cages (25 × 30 cm and 30 cm high) so that they did not become familiar with each other. Once the experiment started, by the second half of February, the birds were put into two groups (12 birds each) in cages measuring 150 × 100 cm and 70 cm high. Food (a granivorous commercial canary mixture supplemented with vitamins) and water were provided ad libitum. Birds were additionally provided with water for bathing. Cages

were outdoors, and so were at ambient temperature and natural day:night regime. The siskins gained weight during captivity (repeated measures ANOVA: mean body mass on capture ± SE: 12.7 ± 0.78 g; in captivity: 14.1 ± 0.95 g; $F_{1,22}=50.43$, $P<0.001$), which suggests that the birds were not under stress while in captivity. The birds were captured and maintained in captivity with the permission of the Subdirecció General de Conservació de la Natura, Generalitat de Catalunya.

Birds were colour ringed for individual identification. We used the size of the black bib badge, which is highly correlated with dominance (Senar et al. 1993), as an indication of social status. This approach has been used in other bird species (Roskaft et al. 1986). This allowed us to correlate dominance with metabolic rate on a large number of birds, without creating an unnaturally large captive flock. We measured the size of the bib on capture by tilting the bird's head back in line with the body, and measuring length and breadth. Badge area was computed a posteriori according to Senar & Camerino (1998). We used keel length as a measure of body size (Pascual & Senar 1996; Senar & Pascual 1997).

For one of the groups, we additionally computed dominance ranks on the basis of agonistic interactions. This allowed us to validate the relationship between dominance, badge size and metabolic rate. We recorded 1838 contests over resources (food, water or perches), within the first 15 days of caging the birds (i.e. when the group was socially unstable; cf. Senar et al. 1990). Birds were observed daily for periods of half an hour per day. In any interaction we recorded the behaviour used by the actor (the initiating bird) and the response by the reactor. The behaviours used by siskins in aggressive encounters are described in Senar (1990) and Senar et al. (1990). We used the resulting data to construct a matrix relating each of the 12 individuals to the number of times that it either used or received the different behaviour patterns. A correspondence analysis based on this matrix produced a dominance score for each individual (see Senar et al. 1994), which we used in subsequent analyses relating dominance to bib size and metabolic rate. Agonistic interactions were recorded after we provided new food. This is when more aggression is seen, with birds establishing queues for food, although they all eventually obtained food. The aggression is similar to that seen among siskins on a bird table: it was never severe, as the majority of the interactions were displays and the majority of encounters were resolved by submission or avoidance or by a bird flying off. Tolerance by the focal birds, allowing other birds to feed in close proximity, was also one of the main forms of agonistic encounter (see Senar et al. 1997).

Once observations on agonistic behaviour finished, the birds were moved by car to the Ventorrillo Biological Field Station (Navacerrada, Madrid, central Spain), at 1500 m above sea level, where we measured metabolic rate. Birds were transported in two cages measuring 100 × 50 cm and 30 cm high, maintained in the dark. Housing conditions in the Field Station were similar to those in Barcelona. The birds stayed there for 2 weeks and were returned to Barcelona where they were released at

the same locality where they were captured. The birds were measured separately but for the rest of the time they stayed in their social groups. We estimated metabolic rate from oxygen consumption (reduction in oxygen volume in the chamber of a respirometer), measured with an oxygen analyser which had a water absorbent in front of it (Binos 100 2M, precision 0.01%; measurement protocol C of Hill 1972; see also Depocas & Hart 1957; Withers 1977; Gessaman 1987). We did a pilot study to select the volume of the chamber and the air flow rate and to measure the temporal variation in oxygen volume in the chamber (according to a Bertalanffy model, $y = a - be^{-x/c}$; Bertalanffy 1960; Kaufman 1981; variance explained by the model = 99.83%, $P < 0.0001$). The time constant in the model (c is the quotient between chamber volume and air flow rate) represents the time that the percentage of oxygen in the chamber needs to cover 63.2% of the whole variation range (the difference between the percentage of oxygen in the chamber at the start of the respirometry measurement and the final value after stabilization). The chamber was a Plexiglas cylinder with a volume of 1700 ml (diameter 18 cm, height 6.7 cm). The air flow rate was 350 ml/min. This gave a slow enough time constant ($c = 5$ min) to ensure the oxygen volume stabilized after 20 min. To ensure accurate measurements, however, we left the birds in the chamber for 40 min. During the last 10 min of this time, we measured the percentage of oxygen of the birds at 2-min intervals (total: six times). We used the average of these six measurements as an estimate of individual oxygen consumption.

All measurements of oxygen consumption were made between 0830 and 1600 hours, at a constant ambient temperature of 20°C (below the thermoneutral zone), with food present in the digestive tract of the birds, when they were not asleep. We replicated measurements of oxygen consumption for each individual five times (we needed about 11–12 days for all the measurements of one individual). The first three measurements were obtained in the dark (i.e. when the bird was not moving about: resting metabolic rate, RMR: Gessaman 1987), and the other two in the light (i.e. when the bird was moving about: fasting metabolic rate, FMR: Gessaman 1987). Light conditions were created using daytime artificial light within the otherwise dark chamber. Dark and light periods were random with respect to time of day. Birds reduced their metabolic rate (either RMR or FMR) during the day, so that a significant time of day effect was detected (two-way ANCOVA on oxygen consumption by individual and according to dark/light conditions; time of day effect: $r = -0.30$, $P = 0.01$; parallelism test for variation on the time of day effect according to dark/light conditions: $F_{1,70} = 2.40$, $P = 0.13$). The order and time of day in which we measured the birds, within and between measurements, was random, so we avoided any significant difference in measurement time per bird ($\bar{X} \pm SD = 12.59 \pm 1.63$ h; $F_{22,23} = 1.230$, $P = 0.31$). The repeatability of measurements of oxygen consumption was higher in the dark than in the light ($r_{i, \text{dark}} = 0.61$, $F_{22,46} = 5.618$, $P < 0.0001$; $r_{i, \text{light}} = 0.38$, $F_{22,23} = 2.201$, $P < 0.033$). In analyses and for each individual, we used the

average value of the three measurements in the dark and of the two in the light. One of the individuals died during the experiment, and was excluded from analyses. The reason for this death is unknown; however, we do not think it was because of our experiment, since no other bird showed any sign of stress. Siskins are very tame birds, so that any manipulation should affect them less than other species.

To measure body mass, we weighed each bird four times between 1145 and 1215 h with a digital balance with 0.01-g accuracy. Different individual measurements spanned 13 days. We used the average of these measurements, which were highly repeatable ($r_i = 0.86$, $F_{22,69} = 24.853$, $P < 0.0001$), and did not vary during the experiment ($F_{3,66} = 0.339$, $P = 0.80$).

No age difference (yearling versus adults) in metabolic rates was detected, either in the light or in the dark (MANOVA: Wilks' $\lambda_{2,20} = 0.90$, $P = 0.33$), and so data from the two age groups were pooled.

Concurrently to obtaining data on the percentage of oxygen consumed in daylight (i.e. last 10 min in the respirometer chamber), we estimated the movement rate of each individual by observing each bird for 10 s every 2 min (total six observations), and adding together the number of movements within the 60 s of measurement. Observations started as soon as we started to obtain respirometry data, and as in the case of the measurement of oxygen consumed, were done twice. We took the average of the two values as an estimate of individual movement rate. Each complete walk around the respirometer chamber or each pivoting on the body was considered as a movement unit; no hop was recorded because of the low height of the respirometer chamber. Other slight movements such as head or wing movements were not considered. The repeatability of movement rate measurement was high ($r_i = 0.73$, $F_{22,23} = 6.380$, $P < 0.0001$). Metabolic rate was therefore controlled for any difference in movement rate between dominants and subordinates in the small respirometer chamber.

We estimated the activity rate of dominants and subordinates in 19 dyads of male birds. We used each bird in just one dyad. These birds were different from those used to record dominance and metabolic rates, although they were trapped at the same time and under the same conditions. Each dyad was housed in a standard cage measuring 150 × 100 cm and 70 cm high and caging conditions were the same as those for the 12-individual group for which we recorded agonistic interactions. We allowed 3 days for each of the dyads to settle into the cage before starting recording sessions. Then, we recorded dominance relationships within each dyad during agonistic encounters from three 30-min daily recording sessions. A bird was considered to be dominant over the other in the dyad if it won significantly more than 50% of the encounters between them, as indicated by the binomial test (Senar et al. 1989). Each dyad was additionally videotaped for 15 min, from which we quantified the four basic energy-requiring movements (walk, hop, run and flight; Mugaas & King 1981; Dolnik & Gavrilov 1982). We recorded the activities of the two birds in a dyad every 5 s for 15 min. Movements such as preening,

calling and pecking were considered accessory (Mugaas & King 1981) and were not included in energy budgets. The basic energy-requiring movements were converted to number of times basal metabolic rate (BMR) according to Dolnik & Gavrilov (1982): walk: $1.45 \times \text{BMR}$; hop: $1.45 \times \text{BMR}$; run: $1.55 \times \text{BMR}$; flight: $12 \times \text{BMR}$; daytime BMR being 39.497 kJ/day. The conversion values were developed for the chaffinch, *Fringilla coelebs*, a similar-sized finch; values may be different for the siskin, but since our purpose was to compare dominants and subordinates we think these values were adequate. The same ethical considerations as for the previous larger group apply here.

Given that bib sizes in the siskin conform to a bimodal distribution not a normal one (Senar et al. 1993), and that activity metabolic rate in the light also departed significantly from a normal distribution (Shapiro-Wilk $W=0.90$, $P<0.02$), we used a rank multiple correlation approach (Conover 1981). This involved carrying out a standard parametric multiple correlation analysis on the ranked values of each variable, thus maintaining the power of the method but avoiding its constraints (Conover 1981). Results hold when using parametric approaches.

RESULTS

Fasting metabolic rate in the light (FMR) was negatively correlated with the size of the siskin's black bib (Fig. 1a, Table 1), which in turn is highly related to dominance (Senar et al. 1993), when we controlled for both body mass and movement rate within the respirometer chamber. Body mass showed a marginal positive correlation with metabolic rate in the light and movement rate showed no correlation (Table 1). The relationship between bib size and metabolic rate in the light remained when we did not control for these factors ($r_{21} = -0.61$, $F_{1,21}=12.37$, $P<0.01$). Resting metabolic rate in the dark (RMR), however, was not correlated with the size of the black bib (Fig. 1b). No correlation was found between metabolic rate in the dark and body mass or movement rate (Table 1). The slopes of the correlations of both metabolic rates with bib size were significantly different (parallelism test: $F_{1,42}=4.74$, $P<0.05$).

The activity metabolic rate in the light was higher than that in the dark (repeated measures ANOVA: $F_{1,22}=56.98$, $P<0.0001$). In the light the oxygen consumption of individuals increased by a mean \pm SD of $20.9 \pm 14.23\%$ with respect to their mean values in the dark (127.1 versus 152.0 ml O_2/h , $N=23$).

Bib size (i.e. dominance) was positively correlated with body mass when controlling for metabolic rate in the light, movement rate in the respirometer chamber and bird size as estimated from keel length (Table 2). The relationship remained when controlling only for metabolic rate. However, this relationship did not appear when no control was undertaken ($r_{21}=0.24$, $F_{1,21}=1.23$, $P=0.28$).

For the group of birds for which we recorded agonistic interactions and computed cardinal dominance scores, the size of the black bib was positively correlated with

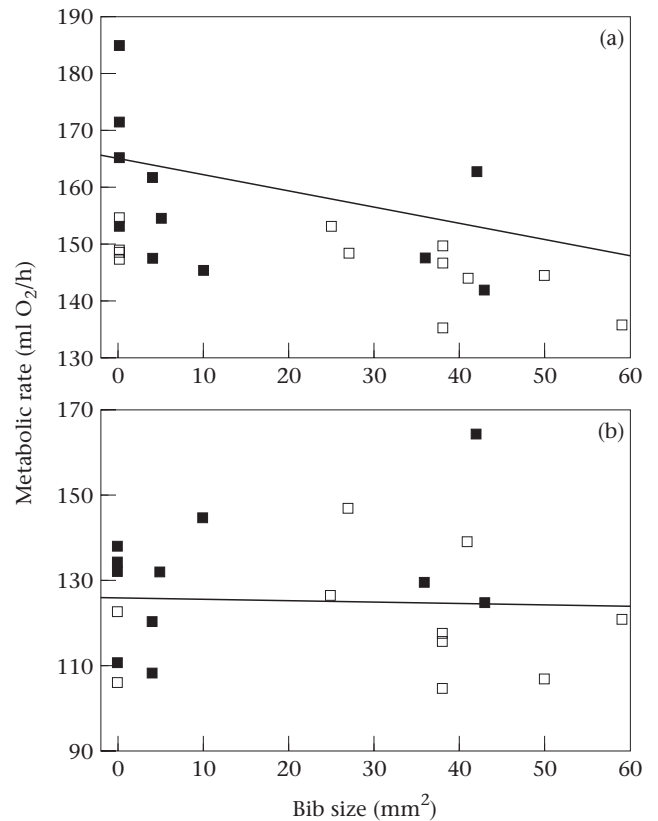


Figure 1. Relationship between siskin bib size and (a) metabolic rate in the light, and (b) resting metabolic rate in the dark (see text for tests; $N=23$ siskins; open and closed squares refer to individuals from the two different groups used).

Table 1. Summary of the multiple regression for the relationship between metabolic rate (in the light and in the dark) and variables bib size (i.e. dominance), body mass and movement rate within the respirometer chamber ($N=23$ siskins)

Variable	Beta	Partial correlation	t_{19}	P
In the light				
Bib size	-0.72	-0.65	3.77	<0.001
Body mass	0.32	0.39	1.86	0.08
Movement rate	-0.08	-0.09	0.41	0.69
In the dark				
Bib size	-0.04	-0.03	0.15	0.88
Body mass	0.02	0.02	0.09	0.93
Movement rate	0.15	0.14	0.61	0.55

For the light: $r=0.69$, $F_{3,19}=5.57$, $P<0.01$; for the dark: $r=0.17$, $F_{3,19}=0.19$, $P=0.90$.

dominance scores ($r_s=0.69$, $N=11$, $P<0.05$), the metabolic rate in the light was negatively correlated with dominance, but the metabolic rate in the dark was not correlated with dominance (Table 3, Fig. 2). A parallelism test, however, was not significant, probably because of the small sample size (parallelism test: $F_{1,18}=0.84$, $P=0.37$).

The metabolic rate of subordinate siskins, as estimated from activity patterns in dyads of birds in cages for

Table 2. Summary of the multiple regression for the relationship between siskin bib size (i.e. dominance) and variables metabolic rate in the light and body mass, controlling for movement rate within the respirometer chamber and bird size as estimated from keel length

Variable	Beta	Partial correlation	t_{18}	P
Metabolic rate in the light	-0.62	-0.66	-3.74	<0.01
Body mass	0.36	0.47	2.23	0.04
Movement rate	-0.27	-0.37	-1.70	0.11
Bird size (keel length)	0.09	0.13	0.57	0.58

$r=0.75$, $F_{4,18}=5.79$, $P<0.01$.

Table 3. Summary of the multiple regression for the relationship between metabolic rate (in the light and in the dark) and variables dominance score, body mass and movement rate within the respirometer chamber

Variable	Beta	Partial correlation	t_7	P
In the light				
Dominance score	-0.96	-0.85	4.30	<0.01
Body mass	0.53	0.64	2.19	0.07
Movement rate	0.15	0.27	0.74	0.49
In the dark				
Dominance score	-0.28	-0.25	0.67	0.52
Body mass	0.17	0.14	0.38	0.71
Movement rate	0.20	0.19	0.51	0.62

The analysis was carried out on a subset of the birds ($N=11$) used in Table 1. For the light: $r=0.69$, $F_{3,7}=8.11$, $P<0.05$; for the dark: $r=0.34$, $F_{3,7}=0.31$, $P=0.82$.

15 min, was marginally higher than that of dominants (repeated measures ANOVA: $F_{1,18}=4.04$, $P=0.06$; $\bar{X} \pm SD$: subordinates: $2.02 \pm 0.64 \times BMR$; dominants: $1.75 \pm 0.64 \times BMR$).

DISCUSSION

Rohwer (1975) proposed that the variation and extent of colour patches in the plumage of many wintering birds could work as badges of social status. Status signalling would be beneficial because it would allow contestants to resolve potential fights without resorting to costly violence (Rohwer 1982). As outlined in the Introduction, a feasible prediction from the status-signalling hypothesis is that as a result of actively avoiding individuals with large badges, which signal their superior fighting ability and therefore save costly fights (Senar & Camerino 1998), subordinates might have a higher metabolic rate than dominants. Our results seem to fulfil this prediction: siskins with small badges (i.e. subordinates; Senar et al. 1993) had a higher metabolic rate in the light than those with large badges, even when controlling for activity rate in the measurement chamber and for body mass. The result also held when we looked at true dominance relationships based on agonistic encounters. Dominance did not seem to entail a reduced muscular tone or any

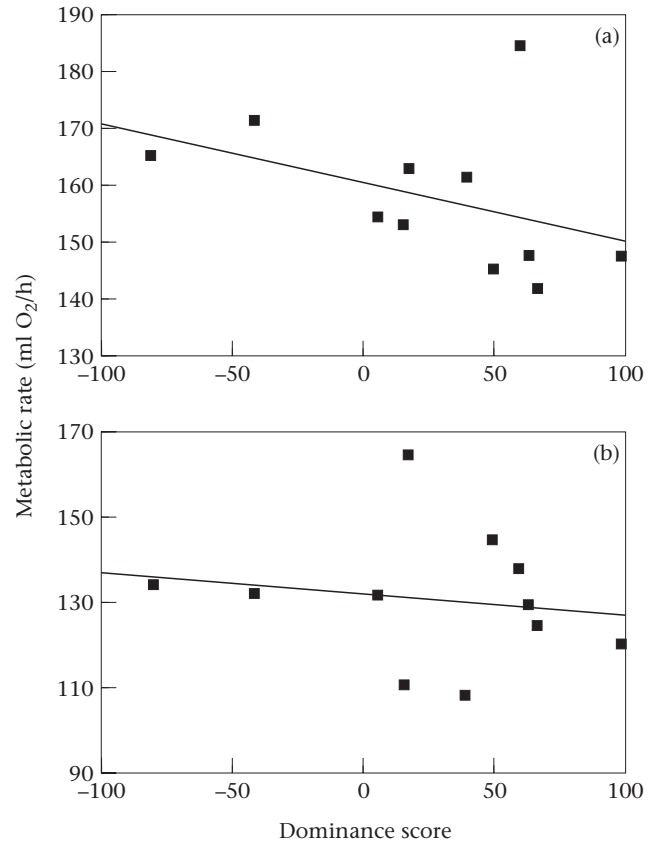


Figure 2. Relationship between siskin cardinal dominance rank and (a) metabolic rate in the light, and (b) resting metabolic rate in the dark (see text for tests; $N=11$ siskins). The higher the dominance of an individual the higher its dominance score.

other physiological adaptation, since no relationship was found between dominance and resting metabolic rate in the dark. The metabolic rates estimated for dyads of caged birds suggest that the difference between dominance classes may be related to their patterns of activity within the flock. Unfortunately, measurement of metabolic rate within a respirometer chamber with birds in isolation does not allow for a direct test of this hypothesis. A better test of this could be to use the doubly labelled water technique (Moreno 1998) to measure the daily energy expenditure of birds with large and small badges (S. Verhulst, personal communication). However, the fact that differences in metabolic rate in the light between dominants and subordinates remained after controlling for movement rate in the respirometer chamber suggests that subordinates may be more susceptible to stressful conditions, so that, when faced with similar situations, subordinates may suffer more stress than dominant birds.

A recurrent point in the status-signalling literature is what mechanism prevents subordinates from pretending to be dominants, by adopting the appropriate but arbitrary badge of status (Senar 1999). One possibility is that these badges are costly to produce and maintain (e.g. Owens & Hartley 1991; Johnstone & Norris 1993). Cheating may be prevented by the high metabolic cost of

dominance (see Introduction; Hogstad 1987; Johnstone & Norris 1993). Our data on siskins, however, show that, at least in this species, the subordinates are the individuals that have the higher metabolic rate. However, we stress that in our study (as well as in other papers), metabolic rate was measured with the birds in isolation and in an equivalent situation. In these conditions, subordinates had a higher metabolic rate, which may mean that any additional activity may be more costly for subordinates than dominants. We may interpret this by relating metabolic rate to a general response to stress. Hence we propose that signalling and maintaining a high social status would be more stressful to a subordinate than to a dominant bird, and so signalling fighting ability would be more costly for subordinates and the status-signalling system can thus easily reach evolutionary stability (Hurd 1997).

Our result that individuals (subordinates) with small badges have a higher metabolic rate contrasts with data from other status-signalling species such as the willow tit, *Parus montanus* (Hogstad & Kroglund 1993) and the great tit, *Parus major* (Järvi & Bakken 1984), in which dominant individuals had a higher metabolic rate (Hogstad 1987; Reinertsen & Hogstad 1994; Roskaft et al. 1986). However, the willow tit data (Hogstad 1987; Reinertsen & Hogstad 1994) were based on birds whose metabolic rate was measured just after capture, and so might have reflected dominance-related differences in stress response to capture and temporary confinement rather than true dominance (Bryant & Newton 1994). Additionally, movement rate within the respirometer chamber was not controlled for. For the great tits, plumage variability was used as an indirect measure of dominance (Roskaft et al. 1986) but this was related to sex and age differences, so that variation in metabolic rates could be related more to sex/age differences than to dominance. There is also some doubt whether the great tit should be regarded as a status-signalling species (Pöysä 1988; Wilson 1992; Senar 1999).

Data from dippers, *Cinclus cinclus* (Bryant & Newton 1994) and salmon, *Salmo salar* (Metcalf et al. 1995), for which a positive relationship between metabolic rate and dominance has been reported, are not directly comparable with the data on siskins because of life history differences between the species. Dippers are territorial and dominant individuals with associated good territories may need a greater effort to maintain them (Bryant & Newton 1994; although the birds did not defend their territory during the measurements, they might have retained their general metabolic rate). The strong relationship between dominance and developmental pathways in salmon may also cause a strong relationship between these two traits and metabolic rates (Metcalf et al. 1995). Data from juncos, *Junco hyemalis* (Cristol 1995), however, are more relevant to our discussion. Juncos had been regarded as a species showing status signalling (Ketterson 1979; Grasso et al. 1996), but the relationship appears only between birds of a different sex or age (Balph et al. 1979). Since the birds in Cristol's (1995) experiment were combined to have the same sex and age, our prediction between status signalling and metabolic rate is not

applicable here. Additionally, there is some doubt whether species in which status signalling does not appear within sex and age classes should still be regarded as showing true status signalling (Whitfield 1987; Senar 1999). Cristol (1995) reported that in socially unstable flocks, in which individuals were unfamiliar to each other, dominants had a higher metabolic rate than subordinates. This may be related to the effort needed by nonstatus-signalling dominants to enforce their dominance and fighting ability. As we have already commented, this is not the case for a status-signalling species, since fighting ability is apparent from the first encounter (Senar & Camerino 1998; Senar 1999).

In juncos, the relationship between dominance and metabolic rate did not hold in socially stable groups with familiar birds (Cristol 1995). This may be because dominant individuals can be recognized, so do not need to enforce their higher status: subordinates just avoid them (e.g. Balph 1977). As already outlined, this situation would be conceptually similar to that of status-signalling species (either in socially unstable or stable groups). So why do dominant and subordinate juncos have a similar metabolic rate rather than a negative relationship? Clearly more data and from more species are needed to understand this variation.

Of direct concern here is the relationship between body mass, dominance and metabolic rate. In several species subordinates weigh more than dominant individuals (e.g. Ekman & Lillendahl 1992; Witter & Swaddle 1995; Hake 1996), while in others the reverse has been suggested (e.g. Baker & Fox 1978; Lundberg 1985; Piper & Wiley 1990). Variation in the relative importance of predation and starvation risks has been proposed to explain these differences, both between and within species (Verhulst & Hogstad 1996). However, a good understanding of the relationship between body mass and dominance requires some knowledge of the effect of social status on energy requirements (S. Verhulst, personal communication). To our knowledge, our work is the first to address simultaneously the relationship between the three variables: our data show that when controlling for metabolic rate, dominants weighed more than subordinates, a relationship that disappeared when we did not control for metabolic rate. This means that dominant siskins carry more reserves than are needed for their daily energy requirements, and so other selection pressures not directly related to metabolic rate may be operating (e.g. flying performance). How far the energy reserves of dominants and subordinates in other species are just a consequence of differences in metabolic rate or are due to other additional selection pressures is unknown. For instance, if dominants are removed from a group, subordinates may lose weight because their food resources become more predictable (e.g. Ekman & Lillendahl 1992), or because their metabolic rate is reduced. Unless we know the relationship between dominance, body mass and metabolic rate in our target species, no prediction may be made.

Clearly more data from more species are needed. In the meantime, our data strongly support the idea that in species in which social status is signalled by plumage

colour, subordinates pay the metabolic cost of social grouping. This may be both because subordinates are more active in monitoring dominants and because they are more susceptible to stress.

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