# Asymmetric contests over resources for survival and migration: a field experiment with bluethroats

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**Abstract.** The relative importance of prior occupancy and of asymmetries in both value of winning and in resource-holding potential for the outcome of animal contests was tested. Bluethroats, *Luscinia s. svecica*, were offered food ad libitum in the field. Prior to migration, at a moulting site, their weight increased rapidly and peaked after a few days. Lean birds won significantly more interactions than fat birds, probably owing to higher motivation to fight for the food. Dominance between individuals shifted and was not correlated with size or prior occupancy. During the subsequent migration, at a stopover site, the bluethroats gained weight throughout their stay. Dominance between individuals was constant and positively correlated with size, whereas fat reserves and prior occupancy had no effect on contest resolution. Fat deposition rates were positively correlated with dominance status. The different dominance patterns are explained in terms of different gain curves of fat for birds putting on fat for survival and migration, respectively. Though prior occupancy had no general effect on dominance patterns, such an uncorrelated asymmetry may have been used to settle single contests between fat birds at the moulting site. The fact that dominance (acting through differences in size) influences fat deposition rates may be important for the spatial and temporal pattern of migration in birds that compete for resources at stopover sites.

Asymmetric contests between two animals may be settled in three main ways (Maynard Smith & Parker 1976). The animals may differ in (1) the value they place on winning or (2) their resource-holding potential, i.e. a contest is won by the biggest, strongest or most experienced individual. These two are often referred to as correlated asymmetries. (3) Asymmetries uncorrelated with resource-holding potential and expected value of winning may be used to settle contests. Prior occupancy, i.e. ownership is always respected by an intruder, is the most commonly suggested example of uncorrelated asymmetries (Maynard Smith & Parker 1976; Maynard Smith 1982).

Many contests may comprise more than one asymmetry. In contests with asymmetries both in resource-holding potential and value of winning, the relative size of the asymmetries will decide the outcome (e.g. Ewald 1985; Hansen 1986; Verrell 1986; Enquist & Leimar 1987; Knight & Knight Skagen 1988). While asymmetries in resource-holding potential are likely to be constant over short periods, asymmetries in value of winning may quickly change. For example, an animal below some critical level of energy reserves will be highly motivated to fight for a food item. However, when the animal has reached that critical level, which

may happen directly upon consumption of that food item, it will no longer accept the cost of fighting (Houston & McNamara 1988). Accordingly, a well-fed individual would probably 'lose' a contest against an individual with a higher value of winning due to, for example, poor energy reserves, even if the latter has a lower resource-holding potential or lower rank (Popp 1987).

Uncorrelated asymmetries are expected to be used for settling contests mainly when correlated asymmetries are absent (Maynard Smith & Parker 1976). However, Hammerstein (1981) showed theoretically that uncorrelated asymmetries may be used to settle contests even when correlated asymmetries are present, especially when the cost of fighting is high in relation to the expected benefit from winning. Maynard Smith (1982) and Grafen (1987) argued that uncorrelated asymmetries, for example prior occupancy, are to be expected mainly in contests over resources with short-term value.

We studied dominance interactions between bluethroats, *Luscinia s. svecica*, competing for food, a short-term resource. They were offered food ad libitum in two different situations. This was first done at a breeding site during the post-breeding moult period when bluethroats normally carry no or only small fat reserves (Lindström et al.

1985). Earlier experiments with captive juvenile bluethroats at this site showed that when fed ad libitum on mealworms, they rapidly put on 3–4 g of fat (Å. Lindström, D. Hasselquist, S. Bensch & M. Grahn, unpublished data). These results lead us to believe that feeding conditions in the wild are normally poor. The second phase of the experiments was carried out at a stopover site during the subsequent migration. We believe that fat deposition at these two sites reflects the two main causes for fat deposition in birds: for survival during periods of low and unpredictable feeding conditions (Johnson 1985; Lima 1986) and as energy reserves for migratory flights (Odum 1960). Houston & McNamara (1988) suggested that energy reserves should be an important factor in deciding an animal's motivation to fight over food resources. In this paper, we investigate how the different use of resources at the moulting site and the stopover site influence the relative importance of resource-holding potential, value of winning and prior occupancy for the resolution of contests.

## METHODS

The bluethroat is a small passerine bird (lean body mass 15 g) that breeds in northern Scandinavia and winters in southwestern Asia (Staav 1975). Prior to autumn migration, adults moult both flight and body feathers whereas juveniles moult only their body feathers (Svensson 1984; Lindström et al. 1985). During moult, birds are very lean and do not store more than 10% fat (% fat calculated as the ratio (total body mass − lean body mass)/lean body mass) before they leave the breeding grounds (Lindström et al. 1985). Migration does not usually commence until moult is almost completed. The first substantial fat deposition takes place at stopover sites in eastern and central Sweden (late August–mid September) before the bluethroats continue their southeastward migration (Stolt & Mascher 1962; Lindström et al. 1985; Ekholm 1988).

We conducted our field experiments at two sites: (1) 27 July–22 August 1987 during the premigratory moult period, at breeding grounds in subalpine birch forest near Ammarnäs, Swedish Lapland (65°58′ N, 16°07′ E) and (2) 27 August–15 September 1988, at a stopover site near Norrtälje (59°46′ N, 18°45′ E), 720 km southsoutheast of Ammarnäs and 300 km from the nearest breeding

area. The stopover area consists of reed beds close to a sewage farm, a typical stopover site for bluethroats. More than 200 bluethroats have been ringed here each autumn since 1980 (Douhan 1986). We shall refer to these two sites as the moulting site and the stopover site, respectively.

Mealworms were offered ad libitum in small bowls (two bowls 100 m apart at the moulting site and one bowl at the stopover site). Almost all bluethroats attracted to the bowls at the moulting site used both bowls. Therefore we pooled data from the two bowls. Activity at the bowls was studied with binoculars from a hide. At the moulting site we made daily observations for about 4 h (at each bowl), normally between 0800 and 1700 hours. At the stopover site we made daily observations for about 3 h in the morning (between 0530 and 1000 hours) and for 2 h in the evening (between 1700 and 2000 hours). All birds that visited the bowls were caught in mist nets and individually colour-marked, and aged, sexed, weighed and their wings measured to the nearest mm (according to Svensson 1984). Moult did not affect wing measurements as the two adults were measured before moulting and as the juveniles did not moult their wing feathers during the study period.

We put the bowl on an electronic balance (Mettler 3000), equipped with an animal weighing function that made the weight records less sensitive to movements of a visiting bird. The birds were weighed to the nearest 0·1 g and their body masses were printed on a Mettler GA44 printer. Thus, we could weigh the birds repeatedly without disturbing them. In the analysis we use weights recorded between 1000 and 1300 hours at the moulting site and between 0600 and 0900 hours at the stopover site.

Bluethroats were regularly involved in aggressive interactions at the bowls. Normally one bluethroat (regarded as the winner) chased another (the loser) from the vicinity of the bowl. Also, if the bluethroat at the bowl warded off an attack and held its position (which happened in less than 5% of the observed attacks), it was regarded as the winner. The sum of all interactions between two specific individuals over the entire period, we call a match. A match could be won (e.g. 7–3), drawn (2–2) or lost (0–14). To get a relative measurement of individual fighting success each bird was given a dominance index. Winning a match scored 2 points, a draw scored 1 point and a lost match scored 0 points. The total score of all matches the bird was

involved in, divided by the number of matches, gave each bird a dominance index between 0 (all matches lost) and 2 (all matches won). In the analysis we used only matches with at least two interactions, and only individuals involved in at least three matches.

To analyse the relationship between body mass and dominance, we divided each individual's period at the bowl into subperiods according to the general pattern of body mass changes (Fig. 1). At both sites, the period until the highest body mass was reached was divided into two subperiods of equal length; at the moulting site, a third period was recognized as the period after peak body mass was reached (Fig. 2). Birds that stayed for fewer than 3 days or were weighed fewer than five times were not included in the body mass analysis. We pooled all interactions the bluethroats were involved in during each subperiod, and calculated for each subperiod the proportion of interactions won. Statistics were used according to Siegel (1956) and Clarke (1980).

## RESULTS

### Observations at the Bowls

A summary of observational data is presented in Table I. Birds that discovered the bowls generally stayed throughout the study period. Thus, the number of bluethroats that used the bowls increased at both sites. Interactions at the bowl sometimes involved physical contact. However, chases without physical contact were more common. Normally a chase ended after just 1–2 m but we often saw vigorous chases that continued for 25–30 m. The bluethroats were not always close to the bowls. This enabled many birds to use the bowls in spite of the presence of a dominant bird in the area.

### Body Mass Changes

At the moulting site, the bluethroats rapidly gained 2–5 g (about 15–30% fat), their weight peaking within a few days (median 3 days, range 1–16, $N = 12$, Fig. 1a–c). Seven birds were omitted from the analysis due to too few weight records. Each remaining individual ($N = 12$) was studied for 16 days on average (range 7–23). After the peak, body mass slowly decreased by on average 0·15 g/ day (range 0·02–0·30 g/day). None of the birds was scored for its highest body mass during the last day it was weighed.

**Table I.** Observations of bluethroats during field experiments at the moulting site (Ammarnäs) 1987 and the stopover site (Norrtälje) 1988
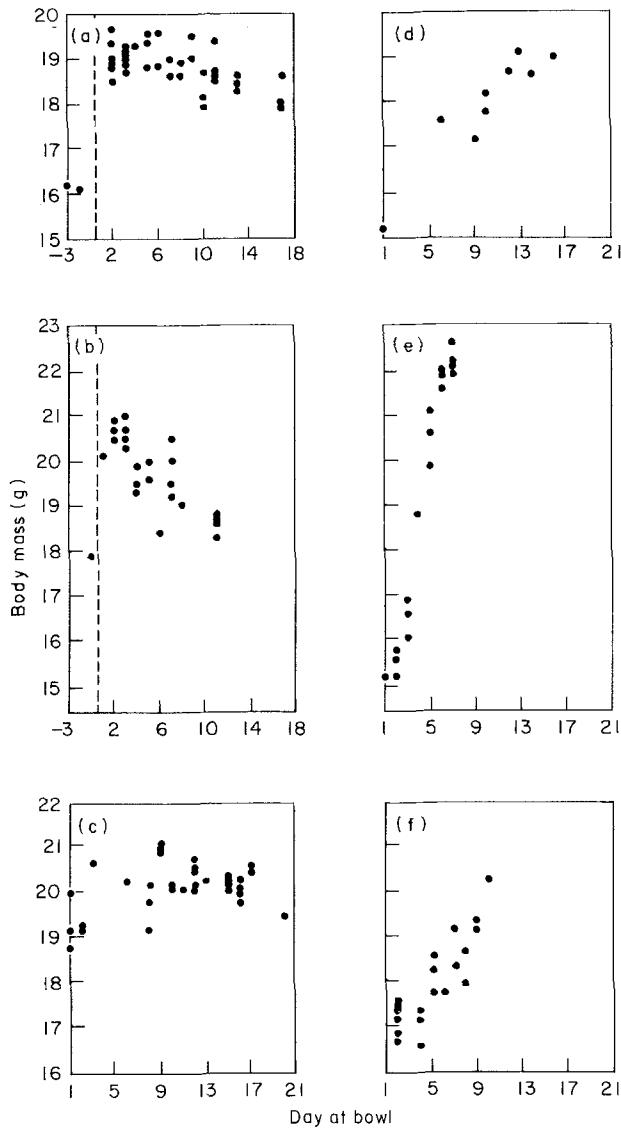
|  | Moulting site | Stopover site |
|---|---|---|
| Hours of observation | 210 | 84 |
| No. of bluethroats | 19 | 14 |
| No. of bluethroats that left within the study period | 2 | 6 |
| Bird visits to bowls | 1439 | 711 |
| No. of days individual birds were studied (median) | 1–23 (11) | 1–15 (5) |
| % Visits involving aggression | 14·5 | 30·1 |
| No. of weights recorded | 525 | 359 |

At the stopover site, all the birds gained weight (2–8 g, about 15–50% fat) throughout their stay at the bowl (Fig. 1d–f). Three birds were omitted due to too few weight records, and 11 other birds were studied for on average 8 days (range 3–15). Seven of them reached the highest body mass on the last day they were studied. This is significantly different from the situation at the moulting site (7 out of 11 versus none out of 12, Fisher's exact probability test, $P = 0·001$). The other four birds reached their highest body masses as follows: on day 2 out of 3, on day 2 out of 4, on day 8 out of 10 and on day 13 out of 16, respectively.

As the birds at the stopover site were studied for on average shorter periods we also compared the birds that had stayed at least 5 days at the bowl at each site. Only two out of nine birds at the moulting site gained weight from day 5 to the last day of observation. This is significantly different from the situation at the stopover site, where all six birds increased their body mass during the corresponding period (Fisher's exact probability test, $P = 0·006$). A contributory cause for the shorter observation periods at the stopover site was that six birds disappeared from the bowls; they probably resumed migration. We conclude that two basically different patterns of body mass changes appeared at the two sites.

### Patterns of Dominance

At the moulting site, interactions were won significantly more often in the first half of the period before peak body mass than both in the second half before the peak (Fig. 2, $\chi^2 = 6·2$, $P < 0·05$) and in the period after the peak ($\chi^2 = 10·2$, $P < 0·01$). At the

**Figure 1.** Examples of body mass changes of some bluethroats feeding at the bowls at the moulting site (a–c) and the stopover site (d–f). Each dot represents a weight record. Two of the birds at the moulting site were trapped near the experimental area once or twice before they started to feed at the bowls. All weights are from 1000 to 1300 hours at the moulting site and from 0600 to 0900 hours at the stopover site.

stopover site, there was no significant difference in the outcome of aggressive interactions between the first and second half of the period at the bowl (Fig. 2, $\chi^2 = 2 \cdot 8$, NS).

The apparent shift in dominance at the moulting site was also seen when we looked at the matches. In 17 out of 28 matches both individuals won at least one interaction each (results were e.g. 7–3 or 2–2).

At the stopover site, one individual consistently won all interactions (e.g. 14–0) in 20 out of 22 matches, i.e. dominance was one-sided. The situation differed significantly between the two sites ($\chi^2 = 13 \cdot 9$, $P < 0 \cdot 001$). Thus, at the stopover site, the dominance relationship between two individuals almost always remained constant throughout the period they were observed at the bowl.
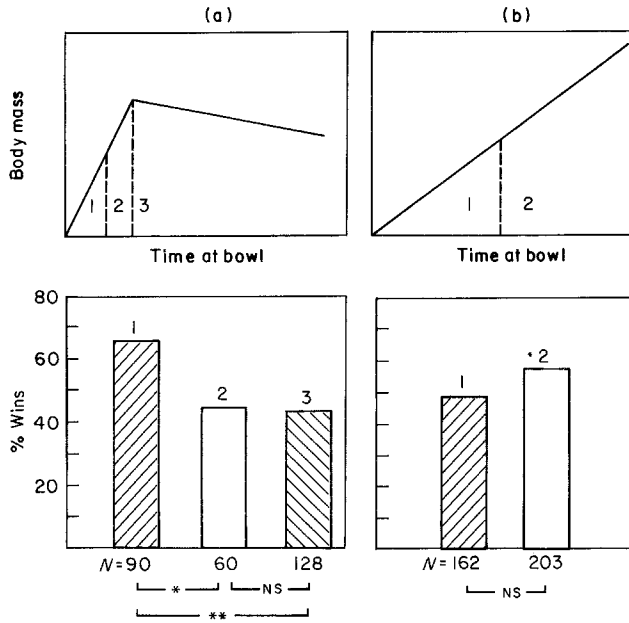
**Figure 2.** Schematic illustration (cf. Fig. 1) of the body mass changes at the moulting site (a) and the stopover site (b). For each bird the period at the bowl was divided into three and two subperiods, respectively. The percentage of interactions won during the different subperiods of 12 individuals at the moulting site and 11 individuals at the stopover site are also shown. Chi-squared test: $*P < 0.05$; $**P < 0.01$.
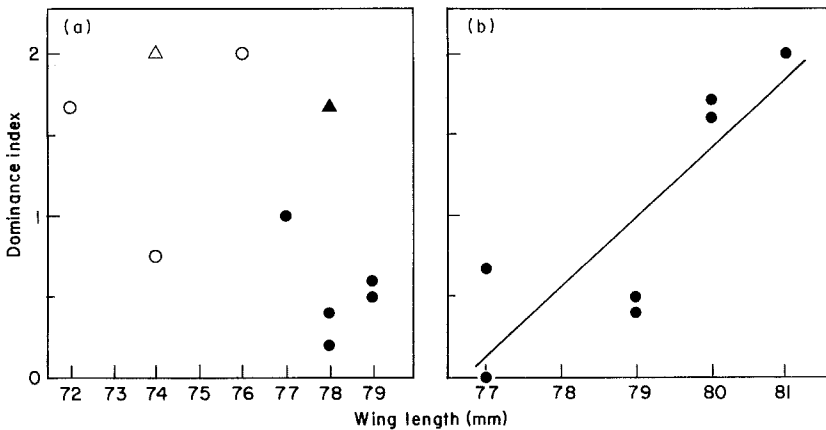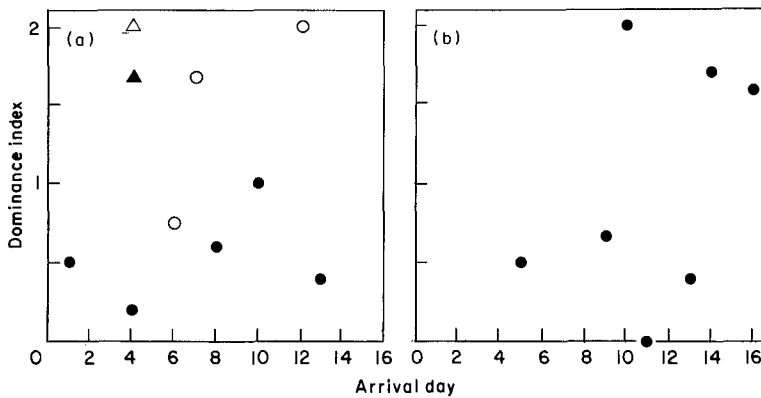


**Figure 3.** Dominance index in relation to wing length of 10 bluethroats at the moulting site (a) and seven bluethroats at the stopover site (b). At the moulting site $r_s = -0.63$, NS; at the stopover site $r_s = 0.83$, $P < 0.05$. For the five juvenile males alone $r_s = -0.05$, NS. The line provides the best fit to the data at the stopover site. ▲: Adult male; △: adult female; ●: juvenile males; and ○: juvenile females.

We could calculate a dominance index for 10 birds at the moulting site (Fig. 3a). There was a negative, though not significant, correlation between dominance index and size (wing length) both in these 10 birds and among the five juvenile males alone. Again, the situation at the stopover site was different. Among seven individuals, all juvenile males, dominance index was significantly correlated with size (Fig. 3b).

The sequence in which individuals started to use the bowl during the study period (prior occupancy) did not affect the outcome of matches. At the

**Figure 4.** Dominance index in relation to arrival day at the bowls of 10 bluethroats at the moulting site (a) and seven bluethroats at the stopover site (b). Day 1 is the day when the first bluethroat started to use the bowls (29 July 1987 and 28 August 1988, respectively). $r_s = 0.07$, NS, at the moulting site and $r_s = 0.18$, NS, at the stopover site. Symbols as in Fig. 3.
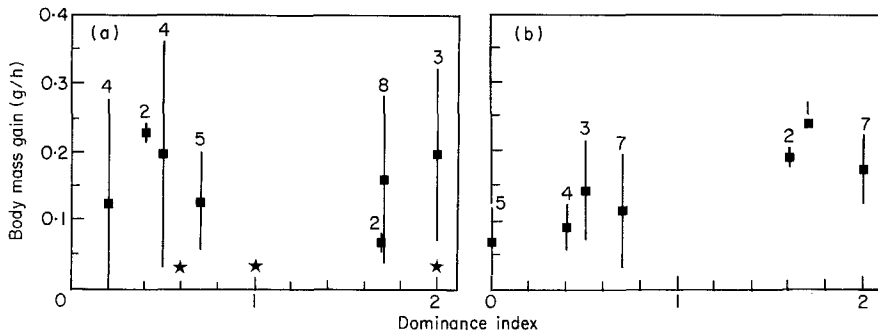


**Figure 5.** The relationship between average body mass gain within a day ($\bar{X} \pm$SD) and dominance index for bluethroats at the moulting site (a) and the stopover site (b), respectively. The figures above the symbols represent the number of days where it was possible to calculate body mass gain. The individuals are the same as in Figs 3 and 4. For three of the birds at the moulting site it was not possible to estimate body mass gains (★). At the moulting site $r_s = 0.03$, NS; at the stopover site $r_s = 0.85$, $P < 0.05$.

moulting site, 11 out of 22 matches were won by the individual that was the first to use the bowl (six matches were drawn), compared to 10 out of 22 at the stopover site. Further, dominance index was not correlated with arrival date at bowls at either site (Fig. 4).

At the moulting site, there was no significant correlation between average daily increase in body mass and dominance index (Fig. 5a). At the stopover site, however, this correlation was significant (Fig. 5b). Also, when comparing relative increase in body mass, i.e. taking body size into account (absolute increase/(wing length)$^3$), higher ranked birds still put on fat at a relatively faster rate and the result from the significance test remains unchanged. Thus, at the stopover site, large blue-

throats dominated smaller ones and deposited fat faster. At the moulting site, there were no significant relationships between size, dominance and average fat deposition rates.

## DISCUSSION

The fat deposition pattern at the moulting site indicated that the food situation there is normally bad. The bluethroats responded to the unlimited food supplies by rapidly storing up to 30% fat. The peaks in body mass that they reached, though, were far below the physiological limit of fat deposition in similarly sized birds. Small passerines regularly put on 50–90% fat when crossing large ecological
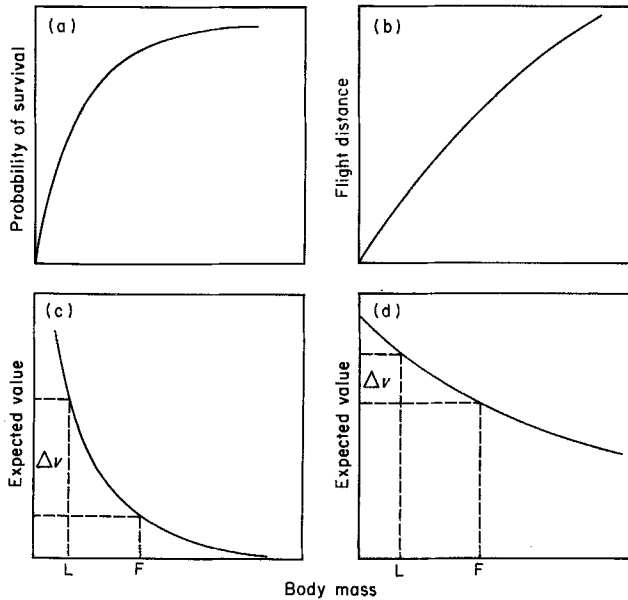
**Figure 6.** Gain curves for a bird putting on fat for (a) surviving harsh and unpredictable feeding conditions (after Lima 1986) and (b) migratory flights (after Alerstam & Lindström 1990). (c), (d) A bird's expected value of extra fat in relation to its body mass. These curves are the derivatives of the gain curves and drawn under the assumption that the expected value of fat is proportional to the marginal rate of gain with increasing fat reserves (body mass). L and F show the expected value of extra fat for two birds with different amounts of fat. Note that the difference in expected value between the two birds ($\Delta V$) is much larger when putting on fat for survival than when putting on fat for migration.

barriers (Alerstam & Lindström 1990). Since the bluethroats seem to refrain from migrating while moulting, we believe that they put on fat mainly to secure survival during periods of unpredictable food supplies. The peaks in body mass may reflect an optimal fat load due to a trade-off between gain in survival and risk of predation (Lima 1986).

Different patterns of dominance relationships were found at the two sites. We believe that these differences were due to dissimilar gain curves for birds putting on fat for survival and migration, respectively.

When putting on fat for survival, the marginal value of additional fat will be very high for a lean bird, but diminish rapidly as fat reserves increase (Fig. 6). For a bird putting on fat for migration the situation is different. Although the potential flight distance a bird can attain will also be a negatively accelerating function of its fat load (due to increasing flight costs), the marginal value of extra fat will not diminish as rapidly as for a bird putting on fat for survival (Fig. 6). If motivation to fight for food is proportional to the benefit of extra fat (value of winning), differences in motivation between birds feeding for survival may be large and change

quickly as their fat reserves change. In contrast, asymmetries in value of winning will be much smaller among birds feeding for migration (Fig. 6).

**Relative Importance of Asymmetries**

In concordance with the model in Fig. 6, bluethroats at the moulting site won more interactions when they had no fat than when close to their highest recorded body mass (Fig. 2). Our interpretation is that animals with low fat reserves (i.e. those in danger of starvation if foraging success happens to fall) are very motivated to fight and win, while at higher fat reserves motivation to fight is very low. The outcome of interactions between two specific individuals often changed throughout the study period and the dominance index was not correlated with size. Instead, it was correlated with an internal variable: fat reserves. At the stopover site, though, dominance between two individuals remained one-sided and the dominance index was positively correlated with size. We conclude that asymmetries in size will be important mainly when contestants are equally motivated, but when asymmetries in value of winning get sufficiently large, the relative

importance of size will diminish. Several studies have shown, or predicted, similar relationships between these two correlated asymmetries (Ewald 1985; Hansen 1986; Verrell 1986; Enquist & Leimar 1987; Popp 1987; Knight & Knight Skagen 1988). At the moulting site we compared body size (wing length) of individuals of different age and sex. Knowing that age and sex can influence dominance patterns (e.g. Ewald 1985), it is possible that clearer relationships might emerge at the moulting site if more data were available.

The uncorrelated asymmetry, prior occupancy, seemed to be unimportant in deciding the dominance patterns in our study. As we studied competition over a resource of short-term value, the use of an uncorrelated asymmetry in settling contests would have been plausible (Maynard Smith 1982; Grafen 1987). Possibly, the expected gain of winning was relatively high in relation to the cost of fighting and thus the correlated asymmetries (resource-holding potential and value of winning) were used to settle contests (cf. Hammerstein 1981). At least this was the case at the stopover site, and in the contests at the moulting site where lean birds were involved. However, an uncorrelated asymmetry might have been important to the outcome of interactions of well-fed birds at the moulting site. We could not test this since, as one might expect, we seldom saw any interactions between these birds. When two or more fat birds were present at the bowl they seemed to line up and wait for their turn. This reasoning is supported by the fact that, at the moulting site, relatively fewer visits to the bowls involved interactions than at the stopover site.

**Implications for Migration Strategies**

In some bird species, individuals frequently get involved in fights to hold territories at stopover sites along their migratory route (Rappole & Warner 1976; Bibby & Green 1981; Mehlum 1983) and there are good indications that birds are unable to put on fat until they have established a territory (Rappole & Warner 1976; Mehlum 1983). Whether bluethroats have stopover territories is hard to unveil due to their skulking behaviour, but they are frequently seen to engage in aggressive interactions (Strindberg 1978; Ekholm 1988; personal observations). In our experiment we found that the dominance index, which varied mainly due to differences in size, influenced the fat deposition rate of bluethroats. Large birds were able to put on fat

at a higher rate than small birds. Thus, the outcome of contests over resources at stopover sites may be set by resource-holding potential and influence a bird's ability to put on fat and eventually migrate successfully. In migrant species where interference competition regularly occurs at stopover sites, we would expect individuals with low resource-holding potential to avoid competition. They could accomplish this in space or time. Interestingly, female bluethroats, being smaller than the males, migrate on average 4–5 days earlier than the males in autumn (Douhan 1986).

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