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Relationships between Body Composition, Body Size and Alternative Reproductive Tactics in a Lekking Sandpiper, the Ruff (*Philomachus pugnax*)

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Summary

1. The Ruff is a lekking sandpiper in which males have two genetically determined alternative mating strategies: 'satellite' or 'independent'. Satellite males are non-territorial, following groups of females on and off leks. Independent males attempt to establish territories on leks and can be either 'resident' territory holders, or non-territorial 'marginals'. The time budgets of the three behavioral tactics (resident, marginal and satellite) differ notably in time allocated to foraging, aggression and display activity. These differences have led to the suggestion that the benefits of size and energy stores may vary with mating tactic.
2. In this paper in vivo estimates of body composition (fat, fat-free mass) for breeding male Ruffs using total body electrical conductivity (TOBEC) are presented.
3. Satellite males have significantly shorter tarsi and wings than independent males.
4. After correcting for size, independent males are significantly heavier and fatter than satellites, and marginals in particular are heavier and fatter than both residents and satellites.
5. Estimates of energy expenditure during flight suggest that satellites may maintain reduced energy reserves to minimize flight costs, while the larger fat stores of independent males are consistent with the benefits of endurance as a territory holder.

Keywords: Fat, FFM, flight costs, TOBEC

Introduction

In many species, larger male body size is associated with greater reproductive success. All else being equal, larger individuals may have an advantage in combat, but body condition and the relative amount of energy stores can also affect the ability of a male to compete successfully (Andersson 1994). In species with alternative mating strategies, intrasexual polymorphism for size is not uncommon (Gross 1996). In some of these species, smaller males also have reduced fitness, but 'make the best of a bad job' by adopting an alternative mating tactic. However, tactic-related size differences are not always associated with differences in reproductive success. Instead, size differences could be the consequence of alternative tactics favoring males with divergent traits. The first step in evaluating whether and how size differences may be selectively advantageous is to describe the body composition of individuals employing alternative tactics to define whether size differences correlate with differences in energy stores.

The Ruff (*Philomachus pugnax*) is a lekking sandpiper in which males have alternative mating strategies (Hogan-Warburg 1966). Breeding males can be broadly categorized as 'independent' or 'satellite' based on

behavior at leks (Hogan-Warburg 1966). These mating strategies also have characteristic time budgets during the breeding season which feature differences in time allocated to foraging, flight and aggression (Lank & Smith 1987; van Rhijn 1991; Höglund, Montgomery & Widemo 1993). Independent males are, or can become, territory holders on leks while satellites typically do not defend territories. Territorial independents, called 'residents,' spend up to 90% of daylight hours on their lek territory, leaving little opportunity to forage (van Rhijn 1991). The mating success of a resident is related to a number of variables including aggressiveness (Widemo 1997) and time spent on the lek territory (Hill 1991; van Rhijn 1991; Widemo 1997). Although the time budgets of satellites and non-territorial independents ('marginals') have not been thoroughly studied, it appears that these males spend more time in flight than residents and have more opportunities to forage since their behavior emphasizes following females on and off leks (van Rhijn 1983, 1991; Lank & Smith 1987; Widemo 1998). Both satellites and marginals are targets of resident male aggression when they do visit leks (van Rhijn 1983, 1991; Höglund et al. 1993; Widemo 1997). Satellites respond submissively (Hill 1991; van Rhijn 1991; Hogan-Warburg 1992; Widemo

1998), while marginal males that are full adults (as opposed to subadults) can potentially be aggressors when they attempt to establish a lek territory (van Rhijn 1991). Satellite males are smaller than independents in measures of total body mass and in estimates of skeletal size such as wing and tarsus length (Höglund & Lundberg 1989; van Rhijn 1991; Lank et al. 1995; this study). Additionally, satellites tend to have a distinctive combination of ruff and head tuft colors, usually white or light colors, and interact in very stereotypical ways with territorial males (Hogan-Warburg 1966).

The differences in mating strategy, time budget and the importance of aggression has led to the suggestion that independent males may benefit from larger skeletal size and greater energy stores (van Rhijn 1991; Lank et al. 1995), while the satellites would not necessarily benefit from larger size, and in fact flight efficiency would favor relatively smaller energy stores (Lank et al. 1995). The data on tactic-related size differences in Ruffs is solely based on measures of total body mass and skeletal size (from captive birds or museum skins). However, these variables do not accurately address differences in energy stores, which are assumed to be mainly in the form of body fat. In this paper we address these issues using in vivo estimates of body composition using total body electrical conductivity (TOBEC) for male Ruffs captured during the breeding season.

Materials and Methods

STUDY SITE

Breeding Ruffs were studied intensively from 1990 to 1997 on the Faludden peninsula in the southern part of the island of Gotland, Sweden (57°10'N, 18°20'E; see Widemo 1995, 1997). In each year, males were captured on leks using cannon nets or mist nets. All individuals were banded and morphological measurements including tarsus length (mm), wing length (mm, maximum chord) and mass (g) were taken. Observations of behavior together with plumage color were used to determine the breeding strategy of each male (Hogan-Warburg 1966; Widemo 1998). In 1992, males first began lekking on April 25, and were still present on June 1. Typically, leks terminate by mid-June. From May 3 to May 19, 1992, estimates of fat-free mass (FFM) were made using TOBEC. Some 71% of all copulations occurred during this period (149/210). The majority of captures (75%) occurred before 08:00 hours.

BODY COMPOSITION ESTIMATES

TOBEC estimates were obtained with an EM-SCAN SA2 (EM-SCAN, Springfield, Illinois). Most birds were

previously marked with both metal bands and plastic color bands for identification. Metal bands affect conductivity so these were removed prior to the measurements (Scott, Grant & Evans 1991), but the plastic color bands had no detectable effect on conductivity and consequently were not removed. Each bird was tucked into a snug nylon stocking with the bill parallel to and resting on the sternum, and the legs folded and tucked into the stocking as well. This posture ensured that the birds were contained safely, and did not move during the measurements. Ten TOBEC readings (hereafter called *E*-values) were taken for each bird, and its position on the delivery plate was checked prior to each reading. Before and after each set of measurements for a bird, a number of readings of a factory set calibration phantom were taken to verify the stability of the EMSCAN. Cloacal temperature in each individual was measured directly after the set of conductivity readings. The temperatures of the 36 Ruffs averaged 40.8°C with a range of 1.7°C. A multiple regression of conductivity on mass and temperature showed no significant partial effect of temperature so this variable was not considered in our analyses.

Ruffs foraging in the study area are exposed to water from the Baltic Sea and in ponds draining cattle pastures. Sea water may affect conductivity (Scott et al. 1991), and a test of the pond water in the study area suggested that this also may affect the conductivity readings. The conductivity was measured of 250 ml of water warmed to 36°C from the following sources: deionized water (DI water), tap water, Baltic Sea, pond water and pond water after recent rain. The average of 10 *E*-values for each was as follows: Baltic sea water = $3,317.1 \pm 19.3$, tap water = 308.3 ± 5.6 , pond water = 247.6 ± 3.5 , pond water just after rain = 172.5 ± 7.5 , deionized water = 29.9 ± 5.0 , empty container = 27.2 ± 3.9 . An ANOVA on these values was significant ($P < 0.0001$), and Scheffé adjusted pairwise comparisons indicated significant differences between all groups except between deionized water and the empty container. Two birds lightly sprayed with pond water and Baltic sea water after an initial set of measurements showed a 1.5% and 18.6% increase in conductivity, respectively. Another two birds were measured after an initial application of DI water, then sea water, then DI water again and showed increased conductivity after the sea-water treatment (average 19% increase from the first DI water values), but the second DI treatment produced results that were within an average of 2% of the first DI treatment. We therefore elected to spray all individuals with Body composition deionized water, especially rinsing legs and leg bands of male Ruffs and allowed them to dry prior to TOBEC estimates to minimize the potentially variable effects of water sources in the habitat.

A species-specific calibration equation relating conductivity to FFM was created using four lekking male Ruffs (three independents, one satellite based on plumage and behavior) captured in Swedish Lapland. TOBEC was measured in these individuals following the procedures described above, after which the birds were killed and frozen for carcass analysis. The entire carcass was macerated, and aliquots were subjected to lipid extraction using the Folch method with chloroform and methanol (Stein & Smith 1982).

The regression of chemically determined FFM and conductivity was significant (Figure 1). It was not attempted to include additional variables (e.g. tarsus

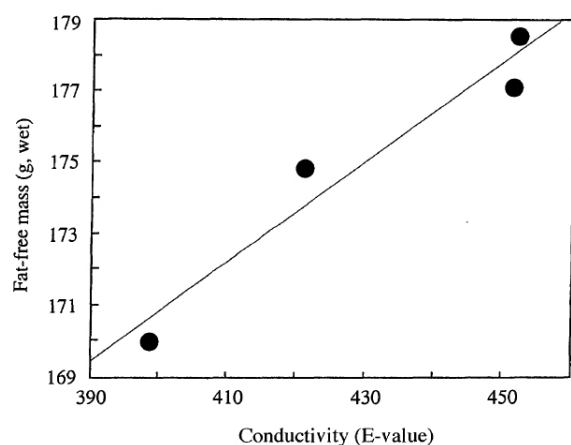


Figure 1. Calibration plot relating FFM to TOBEC (*E*-value). Four male Ruffs were used, ranging in mass from 179 g to 191 g. The dependent variable was selected to be FFM measured by carcass analysis, to directly generate a prediction equation using conductivity measured with the EM-SCAN ($\text{FFM} = 114.7 + 0.14 \times E\text{-value}$, $r = 0.97$, $P = 0.03$).

Table 1. Body composition of breeding male ruffs captured for TOBEC estimates in 1992. Values for independent males (resident + marginal males) are given as a group and separately for each behavioral tactic. Values are means (\pm SD)

	Independent			
	Satellite (<i>N</i> = 7)	Resident (<i>N</i> = 23)	Marginal (<i>N</i> = 6)	Resident \pm Marginal (<i>N</i> = 29)
Total mass, g	206.0 (15.3)	225.9 (12.0)	258.3 (12.4)	232.6 (17.9)
FFM, g	177.3 (6.3)	186.1 (8.0)	190.6 (11.2)	187.0 (8.7)
Fat, g	28.7 (11.5)	39.8 (11.1)	67.7 (7.6)	45.6 (15.5)
Tarsus length, mm	54.8 (2.7)	56.4 (2.7)	56.9 (1.6)	56.5 (2.5)
Residual mass ^a , g	-17.2 (10.9)	-2.2 (12.7)	28.6 (10.2)	4.1 (17.5)
Residual FFM ^b , g	-6.2 (4.9)	0.7 (8.2)	4.6 (10.6)	1.5 (8.7)
Residual fat ^c , g	-10.9 (9.4)	-2.9 (11.4)	24.0 (7.0)	2.6 (15.3)

^aMass (g) = $46.1 + 3.2 \times \text{tarsus (mm)}$, $n = 36$, $r = 0.41$, $P = 0.01$.

^bFFM (g) = $119.1 + 1.2 \times \text{tarsus (mm)}$, $n = 36$, $r = 0.33$, $P = 0.05$.

^cFat (g) = $-73.0 + 2.1 \times \text{tarsus (mm)}$, $n = 36$, $r = 0.33$, $P = 0.05$.

length) in the regression because there were only four points and the residual variation was slight. For the Gotland birds, total body fat was calculated as the difference between total body mass and the FFM estimate using the following equation: $\text{FFM} = 114.7 + 0.14 \times E\text{-value}$ (Figure 1). The range of mass and *E*-values for the birds captured in Lapland does not cover the entire range of variation in the study population though they were typical for Ruff in Lapland (F. Widemo, personal observation). The robustness of our results was examined by reanalysing estimates of FFM using equations for the upper and lower confidence intervals (upper 95% confidence interval: $\text{FFM} = 163.2 + 0.03 \times E\text{-value}$; lower 95% confidence interval: $\text{FFM} = 66.1 + 0.25 \times E\text{-value}$). Though absolute values were different, the values for FFM, fat and their size controlled residuals from regressions on tarsus length produced similar results in terms of statistical significance when relating them to male breeding strategy so it can be concluded that our results are robust.

ANALYSES

Tests comparing body composition between behavioral categories were evaluated by ANCOVA to control for the relationship between skeletal size (tarsal length) and mass. The significance of pairwise comparisons of the ANCOVA adjusted means were evaluated with Gabriel's approximate comparison intervals (Sokal & Rohlf 1981), with the studentized maximum modulus set to a 0.05 significance level. Unless otherwise noted, a male's mass, FFM, and fat estimates are those obtained at his initial capture. Each male is represented once in analyses that pool males captured in different years (maximum *N* = 197).

Results

BODY COMPOSITION: SATELLITES VS. INDEPENDENTS

All estimates of body size and composition indicated that satellite males were lighter and carried less fat than independent males (Table 1; mass, $t = 3.62$, $df = 34$, $P = 0.0009$; FFM, $t = 2.75$, $df = 34$, $P = 0.01$; fat, $t = 2.70$, $df = 34$, $P = 0.01$). In the 1992 sample, independent and satellite males did not differ significantly in tarsal length (Table 1; $t = 1.53$, $df = 34$, NS), but a larger sample collected over all years of the study showed that independent males had longer tarsi and wings (Table 2; tarsus length, $t = 2.85$, $df = 197$, $P = 0.005$; wing length, $t = 2.82$, $df = 193$, $P = 0.005$). These results are consistent with other data sets which show that independent males are skeletally larger than satellites (Höglund & Lundberg 1989; van Rhijn 1991; Lank et al. 1995). Total

body mass, FFM and fat were all significantly related to tarsus length (Table 1). Therefore the relationships between body composition and mating strategy (satellite vs independent) were re-examined while controlling for the effect of size on body composition by ANCOVA. For all tests, the interaction between tarsal length and behavioral category was not significant ($P > 0.4$). Subsequent tests for a mating strategy effect were significant and indicated that independent males had greater mass, FFM and fat for their skeletal size (Table 1; mass, $F_{1,33} = 9.88$, $P = 0.004$; FFM, $F_{1,33} = 5.38$, $P = 0.03$; fat, $F_{1,33} = 5.20$, $P = 0.03$).

BODY COMPOSITION: SATELLITES, MARGINALS AND RESIDENTS

A fine-grained comparison of the three male mating tactics in Ruffs indicated that marginals were substantially fatter than residents and satellites. The 1992 sample did not support differences in tarsal length across the groups (Table 1; $P = 0.6$), but data collected over the

entire study showed that residents had significantly longer tarsi and wings than satellites though marginals were not distinguishable from either group (Table 2; tarsus length, ANOVA $F_{2,195} = 5.601$, $P = 0.004$, Scheffé test; wing length, ANOVA $F_{2,191} = 6.601$, $P = 0.002$, Scheffé test). Size corrected total body mass (i.e. mass residuals; Table 1) was heterogeneous among the different tactics (ANCOVA, interaction $P = 0.3$; group $F_{2,32} = 26.743$, $P < 0.0005$). Comparisons of the mass residuals among groups were significant for all pairs of tactics (Scheffé test, $P < 0.05$) which supports a ranking of males by mass as marginal > resident > satellite. A comparison of size-corrected differences in FFM across all three tactics was not significant, though there was a marginally significant heterogeneity among the groups ($F_{2,32} = 3.31$, $P = 0.05$). However, fat corrected for size (residual fat; Table 1) showed significant group differences by ANCOVA (interaction $P = 0.6$; groups $F_{2,32} = 21.395$, $P < 0.0005$). Pairwise comparisons of the fat residuals for each group indicated that marginal males were significantly fatter than both residents and satellites (Scheffé test, $P < 0.05$), but residents did not have significantly more fat than satellites.

Seven resident males were captured twice during 1992; five of these lost mass between captures (mean capture interval 9 ± 4 days). Daily mass loss averaged $-1.3 \text{ g} \pm 0.6 \text{ g}$ and tended to be different from zero ($t = 2.15$, $N = 7$, $P = 0.07$). There was a similar tendency for daily fat loss ($-0.6 \text{ g day}^{-1} \pm 0.8$, $t = 1.98$, $P = 0.09$) but not for FFM ($0.2 \text{ g day}^{-1} \pm 0.5$, $t = 1.33$, $P = 0.2$).

BODY CONDITION INDICES

The residuals from a linear regression of total body mass on tarsus length are often used as a measure of 'condition' in avian species. The relationship between mass residuals and condition measured as the ratio of fat:total mass was investigated to assess the suitability of residuals as a measure of condition. Using the data from 1992 the mass residuals were positively related to fat:mass ratio (Figure 2). Fat:mass explained 60.7% of the variation in the values for residual mass, validating the latter as a reasonable index of body condition. An alternative index, mass/tarsus³ (Petrie 1983), was not related to fat:mass ratio ($P = 0.13$). A test comparing residual mass across all three male tactics in the pooled data set from 1990 to 1997 indicates that the groups are distinct (Table 2; ANOVA $P < 0.0001$, $F_{2,192} = 18.063$, Scheffé test) as did the earlier comparison of mass residuals for the 1992 data (Table 1). An ANOVA comparing the fat:mass ratio among the mating tactics in 1992 was significant ($P < 0.0001$, $F_{2,33} = 15.582$) and a Scheffé test indicated that the fat:mass ratio of marginal males was significantly greater than both satellites and residents though the latter groups were not

Table 2. Body composition, and skeletal measures of breeding male ruffs captured between 1990 and 1997. Values for independent males (resident + marginal males) are given as a group and separately for each behavioral tactic. Values are means (\pm SD)

	Independent			
	Satellite	Resident	Marginal	Resident \pm Marginal
	(N = 42)	(N = 106)	(N = 50)	(N = 156)
Total mass, g	206.5 (17.1)	221.2 (15.5)	231.7 (26.3)	224.3 (20.2)
Tarsus length, mm	55.1 (2.2)	56.5 (2.5)	55.8 (2.3)	56.3 (2.5)
Wing length, mm	191.0 (3.9)	193.3 (3.3)	191.9 (4.4)	192.8 (3.8)
Residual mass ^a , g	-11.7 (17.4)	-0.6 (15.3)	11.6 (24.4)	3.3 (19.5)

^aMass (g) = $82.2 + 2.52 \times \text{tarsus (mm)}$, $n = 195$, $r = 0.29$, $P < 0.0001$.

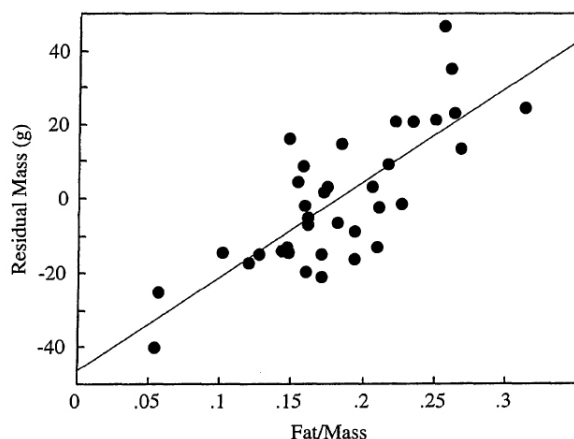


Figure 2. Relationship between mass residuals and body condition (fat:mass). Residual mass = $-46.1 + 253.7 \times (\text{fat/mass})$, $N = 36$ (from 1992), $r = 0.78$, $P < 0.0001$. An equation relating total mass to tarsus length was used to generate residual mass values (Table 1).

distinct from each other which agrees with the results presented for fat residuals in the same sample (Table 1). It is concluded that in this data set, the use of mass residuals provides a less conservative estimate of body condition than comparisons of fat:mass ratio or size-adjusted fat.

Discussion

Previous work has shown that breeding male Ruffs classified as independents are larger than satellite males both in field and captive-reared birds (e.g. Höglund & Lundberg 1989; van Rhijn 1991; Lank et al. 1995). Our data confirm this pattern and further demonstrate that the different male breeding tactics are associated with a characteristic body composition. Independent males have relatively more body fat than satellites, and marginal males in particular have significantly more fat than either residents or satellites (Table 1).

The fat reserves characteristic of males practicing different breeding tactics may result in part from differences in their time budgets. The mating success of resident males greatly depends on the amount of time they are able to spend on their lek territory (van Rhijn 1983; Lank & Smith 1987; Hill 1991; Widemo 1997); all foraging sites are away from the lek. Lank & Smith (1987) report that early in the breeding period, resident males spend most of their time standing on the lek, and only 3.5% of their time foraging. At the peak of breeding residents virtually cease foraging and display occupies up to 40% of their time on the lek. Satellite and marginal males have more foraging opportunities than resident males (van Rhijn 1991; Höglund et al. 1993) and may forage nearly continuously early in the season, dropping to $\approx 20\%$ of the day during the breeding period. The differences in the time budgets between male mating tactics suggest that resident males would lose more mass than marginals or satellites over a given period of time. It was not possible to capture males in the early stages of territory establishment; however, it is possible that independent males will attempt to establish themselves on a lek only when they have acquired large energy reserves—as has been suggested for the Buff Breasted Sandpiper, another lekking shorebird (Pruett-Jones 1988). Our limited sample of recaptures suggests residents lose mass during the lekking period, and the data on body composition are consistent with these predictions. Though similar in size and FFM, the fat reserves of residents averaged 59% that of marginals.

Additionally, our finding that the body composition of resident males was indistinguishable from satellites in most comparisons may not be surprising, since residents would already have depleted some of their

stored fat by the time they were caught. If for some males, the shift from resident to marginal status coincides with a loss of condition to the point that lekking was no longer energetically feasible, it would be expected that some marginal males with levels of body fat lower than residents would be found. All of our captures occurred at leks, so the absence of these hypothetically lean marginals may arise because they spend time at foraging grounds away from leks, and return to leks only when they are prepared to resume territorial activity. It is likely that some individuals in the marginal group were potential resident males, i.e. individuals that attempt to establish territories in a given breeding season (van Rhijn 1983). The relatively large fat stores measured in marginals at these leks may therefore be representative of those of a resident male prior to initiating territorial activity. Clearly, the non-territorial status of marginal males which are visiting leks is not a consequence of poor condition since these are generally the heaviest and fattest males. It is also possible that some of the males categorized as marginals (and some satellites) were migratory birds, which are known to visit active leks en route to other breeding areas (van Rhijn 1991). Given this, the possibility that the large energy reserves seen in the marginals was deposited to fuel subsequent migration cannot be ruled out, but this would not explain the lean condition of the satellites that also visited leks while migrating.

Energy expenditures associated with flight may be a factor affecting the relative costs and benefits of carrying energy reserves. The longer wings of the independent males compared with satellites could promote greater flight efficiency in independents, all else being equal. However, independent males are skeletally larger than satellites as suggested by their longer tarsi, and they have relatively more body fat, both of which could reduce the benefits of longer wings. To estimate energy expenditures during flight, an equation that predicts flight metabolism was used ($\text{kJ h}^{-1} = 3.167 \times \text{mass (g)}^{1.464} \times \text{wing length (cm)}^{-1.614}$; Castro & Meyers 1988). Though not species-specific, this equation has previously been applied to shorebirds (e.g. Butler et al. 1997). Body mass and wing length averages were used for all males (Table 2), and the 1992 study (Table 1) was used for fat:total mass estimates. Using the Castro & Meyers equation, the cost of flight is calculated to be lower in satellites (66.4 kJ h^{-1} , $322 \text{ kJ g}^{-1} \text{ h}^{-1}$) than in independents (73.8 kJ h^{-1} , $329 \text{ kJ g}^{-1} \text{ h}^{-1}$). Across the three behavioral tactics, energy expenditures during flight are greatest for marginals (78.0 kJ h^{-1}) followed by residents (72.0 kJ h^{-1}) and satellites. If independents were to be proportionally as lean as satellites (assuming no change in FFM), their expenditures would be reduced by $\approx 96\%$ to 66.7 kJ h^{-1} ($319 \text{ J g}^{-1} \text{ h}^{-1}$), and their flight metabolism would then be similar to that of an average

satellite male. Conversely, if satellites carried proportionally as much fat as an average independent male (fat:total mass of 0.20 vs 0.14) then a satellite's mass would increase from 206.5 g to 221.1 g which would increase the cost of flight by 10.5% to 73.4 kJ h⁻¹ (332 kJ g h⁻¹). At the same relative fatness, flight costs (kJ g⁻¹ h⁻¹) are greater in satellite males owing to their smaller size, and the overall cost of carrying additional energy reserves increases faster in the smaller satellites so they would pay a relatively greater price for gaining mass. If flight economics are important for satellite males, then this would favor their relative leanness. However, independent males also spend a considerable amount of time in flight. Marginal males, like satellites, appear to travel from lek to lek in the company of females (van Rhijn 1983; Lank & Smith 1987; Höglund et al. 1993), and resident males use a flight display to attract females (van Rhijn 1991). For independent males, and residents in particular, it would seem that flight costs are a less important factor in determining levels of energy reserves than the ability to sustain lekking activity over a long period. In conclusion, our study supports previous suggestions that differences in the body mass of breeding male ruff relate to the needs of flight efficiency as well as the needs of energy reserves to support lekking activity.

Acknowledgements

This study was conducted with permits from the Swedish National Nature Protection Agency (SNV) and the Ethical Committee for Research on Laboratory Animals at Uppsala University (Uppsala Djurförsöksetiska Nämnd). We would like to thank Robert Gibson, Fränzi Huber, Magnus Johansson, Peter Wikström and Staffan Ulfstrand for assistance in finding and capturing Ruffs, and Jacob Höglund for general encouragement. P. R. Evans and I. Scott provided useful suggestions for the use of TOBEC. The field work was funded by the Olle and Signhild Engkvist Foundations, the Swedish Royal Academy of Sciences, and the Uddenberg-Nordingska foundation. This paper was written in part while G.B. was supported by NSF-GIR2813 and F.W. was on a TMR postdoc funded by the European Union, at NTNU in Trondheim.

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