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Fat Storage in Male Willow Warblers in Spring: Do Residents Arrive Lean or Fat?

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Early arrival on the breeding grounds confers important advantages for migratory birds during competition for resources and breeding opportunities (von Haartman 1968, Klomp 1970, Møller 1994, Wiggins et al. 1994). Arriving in good condition also can be important for arctic-breeding birds (Davidson and Evans 1988) because clutch size and timing of breeding may be constrained by parental condition (Rowe et al. 1994). Long-distance passerine migrants arrive at near-arctic breeding sites with larger fat stores than do medium- and short-distance migrants (Sandberg 1996). Recently, Sandberg and Moore (1996) advanced a number of hypothesized benefits to passerine migrants that arrive with extra energy on their breeding grounds, including improved breeding performance, relaxed handling-time constraints, and insurance against adverse conditions. Fat accumulation is not without cost, however. Migrants accumulate fat at stopover sites along migration routes, and time spent foraging at these sites strongly affects overall migration speed (Alerstam and Lindström 1990). Other potential costs that should select against excess fat accumulation include: (1) diminishing return of increased fat depots on potential flight distance (e.g. Lindström and Alerstam 1992) and (2) mass-dependent predation risk due to impaired flight performance and higher exposure to predators during intense foraging (e.g. Hedenström 1992, Houston and McNamara 1993, Witter and Cuthill 1993, Metcalfe and Ure 1995, Kullberg et al. 1996).

Despite the importance of fat, detailed information about fat content in migrant passerines when they arrive at breeding sites and during the transition from migration to breeding is rare (but see Ojanen 1984, Sandberg 1996). In this study, we investigated the amount of visible fat stores in male Willow Warblers (*Phylloscopus trochilus*) on the day they arrived at a breeding site in southern Sweden. The Willow Warbler is a long-distance migrant; birds that breed in northern Europe spend the winter in tropical Africa, some of them as far south as South Africa (Hedenström and Pettersson 1987). We compared visible

fat stores of locally breeding birds with those of birds presumably heading farther north. Furthermore, we measured intra-individual changes in visible fat stores and body mass shortly after arrival to elucidate the dynamics of fat stores during the transition from migration to breeding.

Methods.—This study was conducted during 1992 and 1993 at a 30-ha site located about 1 km from the Baltic shore on the southernmost tip of Gotland Island (56°56'N, 18°11'E; Fig. 1). The site is almost surrounded by the Baltic Sea, and the open-sea distance to Poland in the south is about 240 km. A standardized banding program for migrants has been performed at the site since 1977 by the Sundre Bird Ringing Group (Fransson et al. 1995). Willow Warblers are common spring migrants at this site and make up about 25% of all birds trapped (Fransson et al. 1995).

Trapping was conducted daily from sunrise to noon from about 25 April to 8 June during both 1992 and 1993 using 35 mist nets. Mist nets were visited every 30 min; trapped birds were taken to a field laboratory for measurement and banding. Data collected included maximum wing length (± 1 mm; Svensson 1992), fat score, and body mass (± 0.1 g). Scoring of fat in the furcular cavity and on the belly followed Pettersson and Hasselquist (1985) and included seven stages from 0 (no visible fat) to 6 (belly covered with a thick layer of fat). Cross-checks of fat scores were made regularly among banders to minimize discrepancies (cf. Krementz and Pendleton 1990). Carcass analysis has shown that this visual scoring system, in conjunction with body mass, gives reliable estimates of fat deposition in Willow Warblers (Lundgren et al. 1995).

Most of the Willow Warblers that we trapped probably were on temporary stopover during migration to breeding areas farther north. This is suggested by subsequent recoveries of birds from as far north as 69°30'N in Norway and by short-time recoveries from the Swedish mainland and southern Finland. One banded bird was recaptured a day later about 300 km to the north on an island in the Stockholm archipelago. We assumed that birds trapped during normal banding activities that showed no indication

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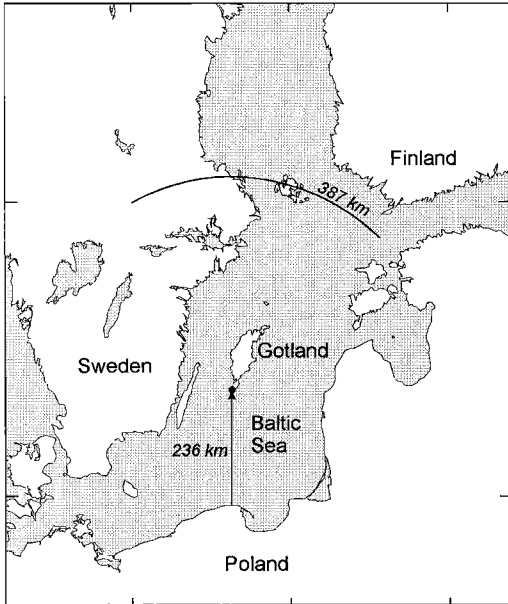


FIG. 1. Map of the Baltic Sea area showing the nearest distance from Poland to southern Gotland (indicated by arrow and dot). A curved line, at a distance of 387 km to the north, is included to indicate the average potential flight distance of male Willow Warblers arriving at breeding sites on southern Gotland.

of belonging to the local breeding population were migrating birds. Males and females cannot be separated based on plumage characters, but they differ in size. We considered individuals with wing length >67 mm to be males (Svensson 1992). In spring, it is not possible to age Willow Warblers based on plumage characters (Svensson 1992).

Male Willow Warblers show a high degree of faithfulness to previous breeding sites (Jakobsson 1988), and about 50% of the males included in this study were banded at the study site during previous years. Males start to defend a territory very soon after they arrive on the breeding grounds, often within hours (Jakobsson 1988). Thus, it was crucial to catch birds as soon as possible after arrival. We therefore kept the study area under close surveillance, especially between 0400 and 1300 when most newly arrived males establish territories. Territorial males display by singing a species-specific song from the top of a small tree and are easy to spot when singing. When a new male was found, we attempted to trap him using song playback, a stuffed Willow Warbler, and a mist net. Captured males were immediately moved to the banding site for examination. Each territorial male was banded with a unique combination of colored leg bands, in addition to a metal band. We tried to retrap each color-banded individual within five

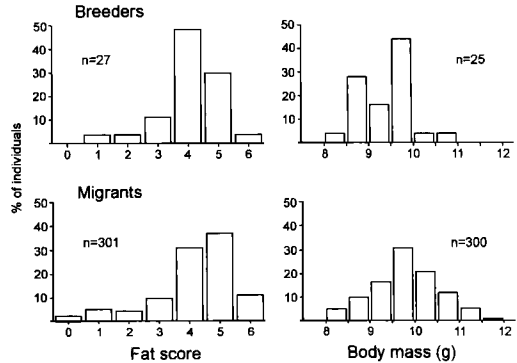


FIG. 2. Distribution of fat scores and body mass of breeding male Willow Warblers at arrival and males trapped while on migration at Skoge, Sundre, Gotland during spring 1992 and 1993.

days of arrival to reexamine its body mass and fat score. We successfully retrapped 15 birds for fat score examination and 14 for body mass (body mass data were missing for one of the retrapped birds).

We calculated predicted flight ranges from individual fat loads using Pennycuik's (1989) program 1, assuming an average lean body mass of 8.5 g and a wing span of 190 mm.

Results.—The median arrival date of locally breeding males that were trapped was 3 May in 1992 ($n = 14$) and 2 May in 1993 ($n = 13$). All but one male had arrived and settled on a territory before 8 May. Wing lengths of breeding males ranged from 68 to 72 mm, and averaged $69.6 \pm \text{SE of } 0.23$ mm ($n = 26$). The passage of migrating males culminated later than the arrival of breeding birds; median trapping dates of migrants were 9 May in 1992 ($n = 193$) and 11 May in 1993 ($n = 112$). The average wing length of passage males was 72.2 ± 0.09 mm ($n = 304$), which is significantly larger than that for breeders ($t = 2.08$, $P < 0.05$), indicating that many of them were headed for breeding sites farther north. In 1992, the body mass of recently arrived breeding males was similar to that of passage migrating males (9.6 ± 0.17 g, $n = 13$ vs. 9.8 ± 0.08 g, $n = 191$; $t = 0.80$, $P = 0.42$). In 1993, the body mass of breeding males (9.2 ± 0.13 g, $n = 12$) was significantly lower than that of passage males (9.7 ± 0.13 g, $n = 109$; $t = 2.36$, $P = 0.02$). Visible fat scores of recently arrived breeding males did not differ significantly from those of migrating males in either year ($t = 0.05$, $P = 0.96$ in 1992; $t = 0.43$, $P = 0.67$ in 1993) and averaged 4.1 ± 0.28 ($n = 27$) for breeders versus 4.2 ± 0.16 ($n = 301$) for migrants. The distributions of body masses and fat scores for breeders and migrating males are shown as combined data for the two years in Figure 2.

Early spring 1993 was characterized by frequent northerly winds, and migrating males arriving before 8 May ($n = 34$) were significantly lighter ($9.25 \pm$

0.12 g vs. 9.66 ± 0.76 g; $t = 9.25$, $df = 119$, $P < 0.01$) and leaner (mean fat score of 3.41 ± 0.22 vs. 4.11 ± 0.13 ; $t = 2.79$, $df = 119$, $P < 0.01$) than males arriving during the same period in spring 1992 ($n = 87$). There was a similar but nonsignificant trend for breeding males to be lighter in 1993. Average body mass of recently arrived breeding males and early passage migrating males did not differ in 1993 (9.2 g for both). Arrival date of breeding males was not correlated with wing length (1992, $r = -0.2$, $df = 13$; 1993, $r = -0.06$, $df = 13$), body mass (1992, $r = -0.26$, $df = 13$; 1993, $r = 0.26$, $df = 12$), or fat score (1992, $r = -0.22$, $df = 14$; 1993, $r = 0.43$, $df = 13$). Among passage migrating males, there was no correlation between capture date and body mass ($r = 0.05$, $df = 189$) or between passage date and fat score ($r = 0.04$, $df = 188$) in spring 1992, whereas both body mass ($r = 0.42$, $df = 109$) and fat score ($r = 0.25$, $df = 109$) were significantly positively correlated with passage date in spring 1993, the windy year. The average body mass of arriving breeding males was 1.1 g (1992) and 0.7 g (1993) higher than the body mass of migrating males with fat scores of 0 to 1 ($\bar{x} = 8.5 \pm 0.13$ g, $n = 9$). This indicates that on average, male Willow Warblers arrive with fat reserves of about 8 to 13% of lean body mass. If arriving males had used their fat reserves for continued flight, they could have flown an additional 387 ± 48 km (range 0 to 978 km) in still air (estimated from program 1 in Pennycuik 1989), which would take them as far as the Swedish mainland north of Stockholm (see Fig. 1).

Fifteen of 25 breeding males were recaptured 1 to 4 days after their arrival ($\bar{x} = 2.7 \pm 0.25$ days, $n = 15$). Their fat scores when recaptured ranged from 0 to 4 ($\bar{x} = 1.6 \pm 0.29$, $n = 15$) versus 1 to 6 ($\bar{x} = 4.2 \pm 0.28$, $n = 15$) when newly arrived (Fig. 3A), a highly significant difference (Wilcoxon signed-rank test, $z = -3.28$, $n = 15$, $P < 0.001$). Males tended to lose almost 1 unit of fat score per day. Only one bird deviated from this pattern. It started off with a low score of 1 and increased to 2 over a 4-day period.

A similar decline in body mass occurred between initial capture and recapture (mean of newly arrived males = 9.4 ± 0.17 g, mean when recaptured = 9.1 ± 0.12 g; Wilcoxon signed-rank test, $z = -2.67$, $n = 14$, $P < 0.01$; Fig. 3B). However, four males did not lose body mass, and two of them even gained mass slightly. One of the birds that gained mass (8.6 to 8.8 g) was the same individual whose fat score increased. The other three birds all had lower fat scores when recaptured, despite no change or a slight increase in body mass (capture vs. recapture; bird A, fat score 4 to 1/body mass 9.3 to 9.3 g; bird B, 4 to 2/8.5 to 8.6 g; bird C, 5 to 1/9.9 to 9.9 g).

The intra-individual changes showed that on average, males lost about 2.5 fat-score units, but only 0.3 g of body mass, which was less than expected from the relationship between extractable fat and fat

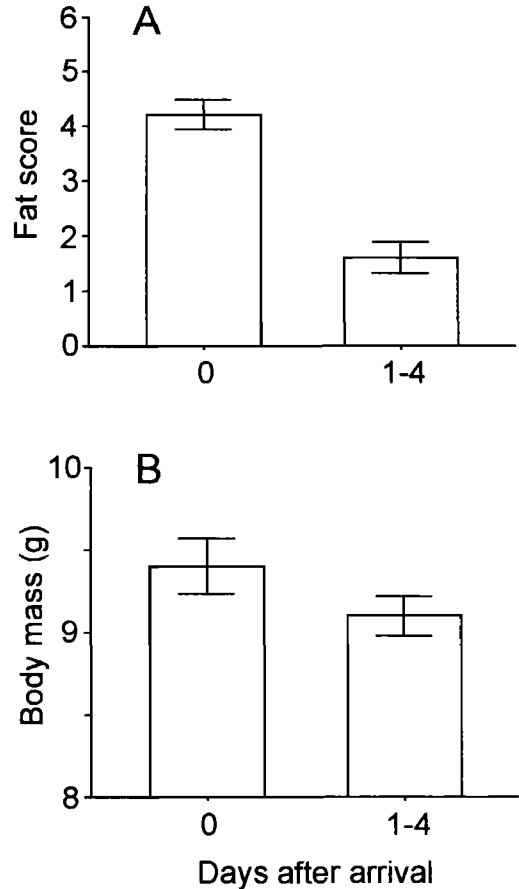


FIG. 3. Mean (\pm SE) fat score (A) and body mass (B) of male Willow Warblers newly arrived to the breeding area and 1 to 4 days after arrival.

score found in spring migrant Willow Warblers (Lundgren et al. 1995).

Discussion.—Our results show clearly that male Willow Warblers arrive at spring breeding sites with appreciable fat reserves that are not much different from those of birds passing through for more northerly breeding sites. Arriving with reserve energy suggests that breeding males devote extra time to fat accumulation during the last part of their migration. This might compromise arriving at the breeding site as early as possible, and even small differences in arrival time may negatively affect breeding (Wiggins et al. 1994, Møller 1994). How much time Willow Warblers devote to depositing extra fat is unclear, but Willow Warblers during spring migration in Britain increase mass at an average rate of 0.4 g/day (Williamson and Butterfield 1954). Furthermore, 11 studies found an average time delay on migratory stopovers, termed "settling cost," of 1.5 days before fat accumulation started (Alerstam and Lindström

1990). This suggests that carrying an additional gram of fat might add three to five days to the Willow Warbler's spring migration.

Because the last migration leg before Gotland involves an extended sea crossing, the residual fuel load carried on arrival might be insurance against bad weather (e.g. headwinds) during migration. A migrating Willow Warbler should, according to Pennycuik's program 1 (1989), use about 0.8 g of fat during a still-air flight of 350 km, which is a reasonable distance for a small passerine to cover during one night. Thus, a sea crossing of about 240 km is well within the range that a Willow Warbler is capable of during a night flight. The observed average fuel reserve at arrival would support an additional 387 km of still-air flight, and thus is larger than would be expected if only serving as a security margin during migratory flight.

Why do breeding males arrive with such large energy reserves? We doubt that these reserves act as insurance against unfavorable feeding conditions on arrival because Willow Warblers normally do not encounter bad weather and poor foraging conditions at this breeding site. It is, however, interesting to note that the fat stores observed in arriving male Willow Warblers at southern Gotland are slightly higher than those reported for male Willow Warblers arriving at breeding sites in northern Sweden at about 66°N (Sandberg 1996). One possibility is that the first days after arrival might be critical for occupying and claiming a territory, and the stored energy makes it possible for a newly arrived bird to devote extra time to territorial behavior rather than to foraging. A breeding male arriving with an extra gram of fat will have about 38 kJ of available energy. The estimated daily energy expenditure of a 8.5-g breeding bird is about 50 kJ/day (Weathers and Sullivan 1989). Apportioned equally over four days, an energy store of 38 kJ would enable a newly arriving male to decrease his required foraging time by about 20%.

The observed loss of body mass during the first few days after arrival suggests a negative energy budget. In one case, we observed a territorial fight between two newly arrived males that lasted for almost a whole day. If a male can establish and hold a territory for a couple of days, he might later have an advantage in terms of prior residency (Krebs 1982, Jakobsson 1988). Whether the observed individual fat loss within individuals, not reflected by the same loss of body mass, can be attributed to some extent to a physiological shift from migratory disposition to breeding activity, remains to be investigated. Such rapid compositional changes, called "phenotypic flexibility," have been demonstrated in several migratory bird species and might, for example, include changes in the digestive machinery (Piersma and Lindström 1997).

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Are Rooster Crows Honest Signals of Fighting Ability?

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Rooster crows are loud, stereotyped vocalizations that appear to function as assertions of social dominance over conspecific males in wild Red Junglefowl (*Gallus gallus*) and their domestic counterparts (Miller 1978, Leonard and Horn 1995). Roosters establish linear dominance hierarchies that reflect individual fighting ability, and dominant males have preferential sexual access to females in a flock (Miller 1978, Leonard and Horn 1995).

Honest signaling theory (Grafen 1990, Zahavi 1991) predicts that assertions of status should entail costs that reveal phenotypic quality, rendering such signals accurate, condition-dependent advertisements of resource-holding potential (Maynard Smith 1982). Costly signals are sometimes referred to as

“handicap” signals (Zahavi 1991, Folstad and Karter 1992). Natural selection should favor honest advertisements of resource-holding potential because both participants in such systems (i.e. signal sender and signal receiver) reduce their risk of unnecessarily engaging in dangerous fighting behaviors. By announcing high resource-holding potential, dominant individuals reduce the incidence of fights and the fitness effects that even victorious animals can face during combat, whereas receivers avoid challenging individuals that they are unlikely to overpower, thereby avoiding injury or death.

Parameters of agonistic acoustic displays produced among males in species as varied as tarbush grasshoppers (*Ligurotettix planum*), toads (*Bufo bufo*),