

## AUTUMN MIGRATION SPEED OF JUVENILE REED AND SEDGE WARBLERS IN RELATION TO DATE AND FAT LOADS<sup>1</sup>

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**Abstract:** We analyzed speed of migration in two congeneric warblers, the Reed and the Sedge Warbler, *Acrocephalus scirpaceus* and *A. schoenobaenus*. Sedge Warblers migrated at a higher speed than Reed Warblers. The two species showed similar rates of fat deposition at our Swedish study site, although Sedge Warblers departed with lower fat loads. The higher speed of migration in Sedge Warblers and their lower departure fat loads suggest that they encounter stopover sites which offer higher relative fat deposition rates farther south. The amount of visible fat at the time of banding was positively related to the speed of migration. Estimates of speed of migration for the two species suggest that the recoveries were situated on average 76–111 km farther south per increase in fat score, corresponding to 58–85% of the expected distance a bird can cover by using the fuel of one unit of fat score.

**Key words:** *Acrocephalus schoenobaenus*, *Acrocephalus scirpaceus*, fat loads, Reed Warbler, ringing recoveries, Sedge Warbler, speed of migration.

For migratory birds, the speed of migration is set by the total time it takes to cover the distance between summer and winter destinations, including stopover time. Speed of migration is expected to vary between different ecological situations depending upon food availability and whether the bird is minimizing the time, total energy expenditure, cost of transport, or risk of predation (Lindström and Alerstam 1992).

Reed Warblers (*Acrocephalus scirpaceus*) and Sedge Warblers (*A. schoenobaenus*) are two closely related species with similar morphology and geographical distribution of both breeding and winter quarters (Cramp 1992). It has been suggested that Sedge Warblers migrate from Northern Europe at a higher speed than Reed Warblers in order to reach important sites for fattening (Bibby and Green 1981). At these sites, situated north of the Mediterranean Sea, high abundance of reed aphids enable Sedge Warblers to build up fat stores sufficient for nonstop flights to tropical Africa (Bibby and Green 1981). In contrast, Reed Warblers, which feed on Diptera, use areas closer to the Sahara including southern Europe and north Africa for

fattening, and the quality of these fattening sites do not deteriorate in the course of the season as much as is the case for the aphid sites used by Sedge Warblers (Bibby and Green 1981). Because Sedge Warblers seem more time stressed, we expected them to migrate at a higher speed than Reed Warblers.

Apart from the difference in diet, the two species exhibit other ecological differences that might be linked to different migratory adaptations: Sedge Warblers lay more eggs per clutch (Bibby 1978) and have a shorter life-span (Peach et al. 1990) than Reed Warblers. The two studies that used banding recoveries did not confirm statistically that Sedge Warblers migrated at a higher speed than Reed Warblers, although both studies reported higher average migration speeds in Sedge Warblers (Hildén and Saurola 1982, Ellegren 1993).

Here, we use banding recoveries and employ multiple regression analyses to examine whether Reed Warblers and Sedge Warblers show different speeds of migration. In contrast to earlier studies, we use a more homogeneous data set because we limit the analyses to juvenile birds banded at one site in south central Sweden. We also examine whether fat load at the time of banding is correlated with the speed of migration.

### METHODS

We used banding recoveries of birds banded at Kvismare Bird Observatory (59°10'N, 15°25'E) between 1982 and 1995. Each year the banding was conducted between late June and late September at two to four different sites in the Kvismaren-Hjälmaren area (maximum distance between sites 15 km). Birds were aged according to Svensson (1992). The amount of visible fat in the furcular cavity and belly was scored on a scale between 0 and 6 (Pettersson and Hasselquist 1985).

In total, 20,661 juvenile Reed Warblers and 8,354 juvenile Sedge Warblers were banded. Our banding effort resulted in 111 and 36 recoveries, respectively, during the birds' first autumn migration through Europe. In order to exclude birds not yet migrating, we only included birds recovered south of the banding site, at a distance of at least 50 km and with a migration speed exceeding 10 km day<sup>-1</sup> (Hildén and Saurola 1982, Ellegren 1993). We also restrict analyses to birds that were scored for fat loads at the time of banding. This reduced data set consists of 85 Reed Warbler and

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31 Sedge Warblers. Most recoveries (95%) involve recaptures by other banders.

Statistical tests were done in SYSTAT (Wilkinson 1992), and all  $P$ -values are two-tailed tests. When we applied multivariate statistics, residuals were approximately normally distributed. We used distance from the banding site as the dependent variable and date of banding and recapture as independent variables. Residual distance should hence be analogous to speed of migration. We chose to use distance as the dependent variable rather than speed because the latter is a ratio (distance/time) showing nonlinear relations with both banding and recapture date. If not otherwise stated, we report mean  $\pm$  SD.

## RESULTS

The average speed of migration was  $55.3 \pm 30.7$  km day<sup>-1</sup> for Sedge Warblers ( $n = 31$ ) and  $38.8 \pm 24.4$  km day<sup>-1</sup> for Reed Warblers ( $n = 85$ ), and the difference is significant (ANOVA,  $F_{1,114} = 8.94$ ,  $P < 0.01$ ). The two species did not differ in date of banding (7 versus 11 August,  $t$ -test,  $t_{114} = 1.24$ ,  $P > 0.2$ ) or in the number of days elapsed between banding and recapture ( $20.1 \pm 8.7$  versus  $20.5 \pm 9.4$  days,  $t_{114} = 0.19$ ,  $P > 0.5$ ). However, the distance to the recovery site differed between species (Sedge Warblers:  $1,078 \pm 607$  km versus  $770 \pm 519$  km for Reed Warblers,  $t_{114} = 2.71$ ,  $P < 0.01$ ).

For both Sedge and Reed Warblers, we found that the date of banding and the date of recovery had significant effects on the distance to the recovery site (all  $P$ s  $< 0.001$ , based on multiple regression analysis). In neither of the species was the interaction term between date of banding and date of recovery significant, suggesting that the effect of recovery date on distance is the same, independent of when the banding was done, and vice versa.

In Reed Warblers, the distance to the recovery site decreased by  $32.7$  km day<sup>-1</sup> of banding and increased by  $37.8$  km day<sup>-1</sup> of recovery. In other words, for a given recapture date, birds will on average be encountered  $32.7$  km closer to the banding site for each day later in the season they were banded. Similarly, for a given banding date, birds will on average be encountered  $37.8$  km farther south of the banding site for each day later in the season they were recaptured. The corresponding values for Sedge Warblers were  $43.4$  and  $63.1$  km day<sup>-1</sup>, respectively.

The variables banding date (ANCOVA;  $F_{1,110} = 60.7$ ,  $P < 0.001$ ), recapture date ( $F_{1,110} = 76.9$ ,  $P < 0.001$ ), and species ( $F_{1,110} = 4.67$ ,  $P < 0.05$ ) were significant, as was the interaction between species and recapture date ( $F_{1,110} = 4.86$ ,  $P < 0.05$ ). This supports the conclusion that Sedge Warblers migrated at a higher speed than Reed Warblers.

Figure 1 graphically depicts the relation between predicted speed of migration and date of recovery for birds banded at three different dates. For both species, the speed of migration seems to increase the later the bird has been banded. Birds banded early have an initially low speed of migration which later increases until it reaches an asymptotic speed. Conversely, birds banded late have an initially high speed of migration which later drops to an asymptotic level. This obser-

vation probably arises due to two circumstances (Fransson 1995). Many birds banded early in the season may not have started migration and will thus contribute to the initially low recorded speed of migration. Late in the season, on the other hand, many birds will be captured with filled fat loads, and if recovered soon after banding, they may have covered a considerable distance. The recorded asymptotic speed of migration will be reached when one or several full migratory episodes (stopover time plus migratory flight) have been completed.

The multiple regression model described above can be used to control for the effect of banding and recapture date on how far south the birds were recovered (residual distance). By adding fat score to this model, we can examine whether the amount of fuel the birds carry at the time of banding may further explain the distance to the recovery site. For Reed Warblers, fat score significantly increased ( $P = 0.03$ ) the proportion of variance explained ( $R^2 = 0.47$  for the model including fat score). The slope of the regression (mean  $\pm$  SE) suggests that the distance to the recovery site increased by  $76.0 \pm 34.1$  km per fat score. Similarly, when we added fat score of Sedge Warblers to the multiple regression model, it tended ( $P = 0.07$ ) to increase the explanation of the variance in distance ( $R^2 = 0.59$  for the model including fat score). The slope suggests that the birds were recovered  $110.9 \pm 59.3$  km farther south per fat score.

## DISCUSSION

### SPEED OF MIGRATION

The present study confirms the suggestion that Sedge Warblers migrate at a higher speed than Reed Warblers (Bibby and Green 1981). The reason why Ellegren (1993) did not find a significant difference in speed of migration between the two species even though he analyzed a larger data set, which partly included the one we examined here, might be that he combined recoveries from several banding sites. This possibly increases the variance of the means, because locales may differ in the proportion of birds molting/staging and migrating.

In general, the speed of migration increases with the migratory distance (Ellegren 1993). At Kvismaren, juvenile Sedge Warblers have a more restricted first pre-basic molt than Reed Warblers which allows them to leave the breeding ground at an earlier date (Hall 1996). The difference in speed of migration between birds banded late in the season (Fig. 1), suggests that the observed higher speed of migration in Sedge Warblers is not a consequence of a later start of migration in Reed Warblers. How do Sedge Warblers accomplish migration at a higher speed than Reed Warblers?

The flight speeds of the two species are probably very similar because they differ very little in wing morphology and mass (Hedenström and Møller 1992), the most important parameters determining flight speed (Pennycuik 1989). Given that the two species are equally good at selecting favorable winds, difference in speed of migration is likely to reflect differences in time spent at stopover sites (Lindström and Alerstam 1992). There are at least two mechanisms by which total stopover time might be shorter in Sedge than in

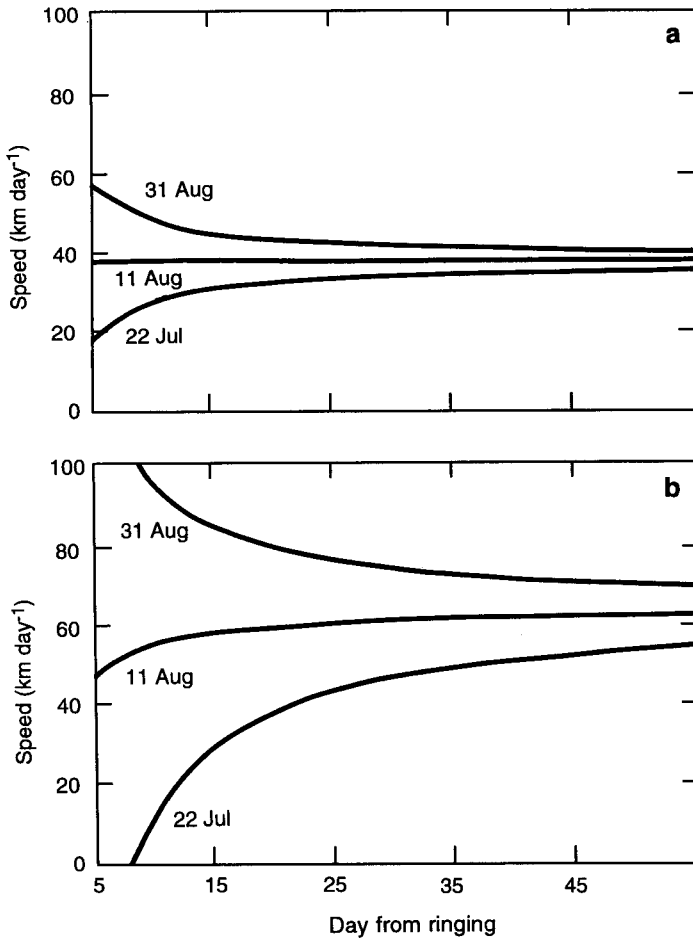


FIGURE 1. The numerical solutions of the models (see text) showing the relationship between speed of migration and number of days between banding and recovery for (a) Reed Warblers and (b) Sedge Warblers banded at three different dates (22 July, 11 August, and 31 August). The relationships have been obtained by dividing the expected values of models by time between banding and recapture.

Reed Warblers: Sedge Warblers may be more efficient in finding good feeding sites and, having found a feeding site, may have a higher rate of fat deposition than Reed Warblers.

The first mechanism is difficult to test because it requires knowledge of how much time it takes until a bird has found the site at which it stays for fat deposition. However, because the two species use similar habitats for stopover (Cramp 1992), there is no reason to expect that it would take longer for Reed Warblers to find a suitable stopover site.

At our Swedish study site, Reed and Sedge Warblers appear to show the same rate of body mass change, indicating a similar fat deposition rate (Hall 1996). Hence, data on fat deposition rates at Kvismaren cannot explain the difference in speed of migration between the two species. Sedge Warblers would manage to maintain a higher speed of migration than Reed

Warblers if their stopover sites south of Kvismaren allowed them to keep a relatively higher fat deposition rate. Both the time-minimization hypothesis and total energy minimization hypothesis (Lindström and Ålerstam 1992) predict that Sedge Warblers should leave Kvismaren with lower fat loads than Reed Warblers if they expect to encounter relatively higher fat deposition rates farther south along the migratory route. In agreement with these two hypotheses, Sedge Warblers depart from Kvismaren with lower fat loads than Reed Warblers (Hall 1996). Unfortunately, there are only limited data available on fat deposition rates along the migratory route of Swedish Reed and Sedge Warblers. However, Sedge Warblers of Scandinavian origin do not put on fat in northern Italy (Basciutti et al. 1998), suggesting that the presumably important areas for fattening could be located farther south in Europe or in North Africa.

## FAT LOADS

In general, birds with large fat loads are capable of flying longer distances than birds with smaller fat loads (Pennycuick 1989). At present, there are no data available on how our fat scores relate to mass of fat in *Acrocephalus* warblers. For Willow Warblers (*Phylloscopus trochilus*) in autumn, one unit of fat score corresponds to 0.26 g of fat (Lundgren et al. 1995). Lean mass of Reed and Sedge Warblers at Kvismaren is 10.8 g for both species (Hall 1996), whereas lean mass of Willow Warblers is 7 g. By scaling up, one unit of fat score in the *Acrocephalus* warblers would correspond to 0.40 g of fat. One problem with converting fat scores to actual fat is that the relationship is likely to be nonlinear (Kaiser 1993). For simplicity however, we assume that one unit of fat score corresponds to 0.4 g of fat in both species.

Passerines are predicted to consume fat at a rate of about 1% of their body mass per hour in migratory flight (Nisbet et al. 1963). One unit of fat score should then be enough for 3.7 hr of flight. Assuming a ground speed of migration of 35 km hr<sup>-1</sup> (Alerstam 1982), the bird might be able to cover a distance of 130 km in calm conditions. We found that recoveries of Reed and Sedge Warblers on average were situated 76 and 111 km farther south, respectively, per increase in fat score at banding. These values correspond to 58% and 85%, respectively, of the expected distance a bird can cover by using the fuel of 0.4 g fat. We acknowledge that the above calculations are approximate, but nevertheless, our results suggest that of two birds being at a stopover site on any given day, the one with the larger fat loads will migrate ahead of the leaner bird. For both these species wintering in West Africa, this difference may have fitness consequences as early arrival to the winter quarters allows an early start of the prealternate molt, enabling birds to complete molt before the oncoming dry season (Bensch et al. 1991).

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