Extreme fattening by sedge warblers, *Acrocephalus schoenobaenus*, is not triggered by food availability alone

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The strategies adopted by birds during migration are expected to be strongly influenced by resource availability and the efficiency with which these resources are used. The migratory strategy of the sedge warbler in northwest Europe has been linked to superabundances of plum-reed aphids *Hyalopterus pruni* that enable birds to accumulate extensive fat reserves and make nonstop flights to sub-Saharan Africa. Food availability was therefore expected to be the main determinant of whether sedge warblers accumulated extensive reserves or not. In this study, birds were provided with an unlimited supplementary food source, but only 10 out of 24 birds accumulated large reserves. In view of this, temporal and geographical cues reflecting seasonal variations in aphid abundance are considered, in addition to food availability, to determine whether extensive fuelling occurs. Optimality models of resource use by migrants predict two modes of fuelling behaviour, as seen here, if strategies have evolved to divide a journey into an optimal number of stages or if the perception of resources at future sites varies between birds or in time/space. If sedge warbler perception of future resources reflects the temporal and geographical variation in aphid abundance in northwest Europe, then the distribution of fuelling behaviours observed here is expected. Despite some birds accumulating large fuel reserves, they did not show a high degree of sensitivity to wind conditions when initiating migratory flights.

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Migration is an energetically demanding process and consequently migratory strategies are expected to be influenced by the ability to utilize various food supplies and the distribution of those supplies both in space and time (Alerstam 1990). The contrast between two migratory birds, the reed warbler *Acrocephalus scirpaceus* and sedge warbler illustrates this principle. Sedge warblers perform a remarkable long-haul migration from northwest Europe to sub-Saharan Africa by feeding extensively on superabundant food supplies, specifically reed aphids (e.g. *Hyalopterus pruni*), while the reed warbler must stop and refuel two or three times to complete the same journey. This difference arises because reed warblers are less efficient at preying on reed aphids despite considerable ecological and morphological similarity to the sedge warbler (Bibby & Green 1981).

While sedge warblers stopover for long periods and accumulate enormous fuel reserves (80–120% of their lean body mass) in some reedbeds in northwest Europe, the proportion doing so can be relatively small. Indeed, when aphid abundance is low, up to 85% of birds may remain at a site for 2 days or less, accumulating only small reserves (Bibby et al. 1976). This suggests that the spatial distribution of resources, i.e. reed aphids, influences fuelling behaviour and that short stays and consequent rapid movements between sites are a searching behaviour adopted by birds looking for a resource rich reedbed (Bensch & Nielsen 1999; Wernham et al. 2002). However, even where aphid infestations occur not all birds remain to fuel extensively (Bibby & Green 1981), suggesting that other factors influence which behaviour is adopted.

Optimality models have been used to examine how migrants should respond to resource availability under various selection pressures during stopovers/fuelling periods (cf. Alerstam & Hedenström 1998). The stopover behaviour of several long-distance migrants is consistent...
with time-minimization (Bayly 2006) and given the restricted temporal availability of reed aphids, whose abundance peaks in early August in the U.K. and is in rapid decline by late August (Bibby & Green 1981), the same is likely to be true of sedge warblers. While time-minimizing models predict that fuel loads will increase with resource availability/fuel deposition rate (FDR), stopover durations are expected to decrease, not increase as is true of sedge warblers (Alerstam & Lindström 1990). However, varying the assumptions of the model can change the outcome: for example, if migratory distance is considered finite then a stepped function arises because the journey is best divided into equal steps, rendering the same fuel load optimal over a range of FDRs (Weber & Houston 1997). In this case, fuelling duration increases in steps with FDR. Alternatively, fuel loads and fuelling durations are predicted to increase if decreasing resources are expected at future sites (Weber & Houston 1997). In addition to resources, weather is expected to influence stopovers (Weber et al. 1998) and given the extremely large reserves laid down by sedge warblers, they are expected to be highly sensitive to wind conditions and to delay departure until conditions are favourable (Liechti & Bruderer 1998).

To examine how resources influence fuelling behaviour, free-living sedge warblers were attracted to an unlimited supply of food at a reedbed in the U.K. and their body mass was recorded daily. The departure mass of birds utilizing the food source was expected to reflect extensive fuelling if abundant resources were the cue for this strategy. The departure loads and FDRs of experimental birds were compared to time-minimizing models to determine whether birds were responding to resources in an optimal way. In conjunction with weather data, the sensitivity of departure decisions to wind conditions was also tested.

METHODS

Study Site

The Pannel Valley Reserve (PVR) is located in southeast England (50°54′N, 0°41′E) and consisted of a 23 ha mosaic of Phragmites reedbed, sallow Salix scrub and open water, 1.7 km from the English Channel. Daily mist-netting at PVR between July and October has resulted in a mean annual capture of 7965 sedge warblers (mean of 1995–2004).

Food Supplementation Experiments

Sedge warblers were attracted to supplemental food during 1 August–16 September 2001, 12 July–30 September 2002, 6 August–2 September 2003 and 26 July–12 September 2005. Food was presented in a feeder consisting of a wooden box (25 × 40 × 15 cm) attached to a stake (0.7–1.5 m high), driven into the ground within the reedbed (Fig. 1). A plastic bowl (10 × 4 cm), kept topped up with at least 50 mealworms, Tenebrio molitor, from dawn till dusk, was inserted into a purpose-made hole on the box top. Feeders sometimes had to be emptied overnight to avoid consumption by small rodents. This set up is similar to that used in previous studies (e.g. Fransson 1998; Bayly 2006) and is expected to give comparable results. In 2001 and 2002 birds discovered the feeders by chance, while in 2003 and 2005, sedge warbler song was played close to unattended feeders during the morning to increase the rate of discovery.

Body Mass Recordings

Body mass, which reflects the mass of stored fuel (Redfern et al. 2004), was recorded using an electronic balance inserted into the feeder box (Ohaus Scout II, Ohaus Corporation, Pine Brook, NJ 07058, U.S.A.; Fig. 1) and a video camera (Sony CCD-TR748E Hi8, Sony Corporation) according to the methods described in Bayly (2006). Remote weighing avoids the potentially confounding effects on body mass and foraging behaviour associated with catching and handling birds (e.g. Gosler 2001).

Recordings were made twice daily between 0700 and 1000 hours and 1700 and 2030 hours, with filming sessions lasting ca. 45–90 min. Where possible, evening recordings were made in the hour preceding sunset. Videotapes were analysed on a colour television and the identity, time of visit (to the nearest minute), body mass (to the nearest 0.01 g if possible, otherwise to 0.1 g) and the number of mealworms consumed on each visit were recorded. Some individuals could be identified either because they had a unique combination of colour rings or because of a combination of the following features: the presence/absence of a metal ring, small plumage differences, and by marked differences (>1.5 g) in body mass (e.g. of 24 birds: colour rings: two juveniles; metal ring: 10 juveniles, one adult; no ring: 10 juveniles, one adult). Individuals that could not be confidently identified were excluded from the analyses. Licences for the trapping, ringing and colour ringing of birds were obtained from the British Trust for Ornithology.
Fuel Deposition Rates, Departure Loads and Intake Rates

Departure loads and three measures of FDR were calculated using the following equations where LBM stands for lean body mass (N.B. values could not be calculated for all birds):

overall FDR = (mass change between first and last evenings/days fuelling)/LBM;
initial FDR = (mass change between 1st and 3rd evenings/days fuelling)/LBM;
hourly FDR = (evening mass – morning mass)/hours in between.

Departure load = (body mass on last evening – LBM)/LBM

Evening body mass was defined as the mean of all mass recordings in the 30 min prior to a bird’s last feed of the day. If recordings did not include this 30-min period, evening body masses were extrapolated using a linear regression (a linear model provided the best fit to regular mass recordings from an individual over the course of a day). Starting body mass was that recorded on the first evening of a bird’s attendance at a feeder, except in two cases where birds did not initially gain mass (instead, the start of fuelling was defined as the day before two consecutive days with gains of >1 g/day). LBM was estimated from a regression model of body mass on wing length using sedge warblers with a fat score of zero trapped at PVR in 2005 (regression: LBM = 0.706 + 0.144 x wing; \( P_{1.708} = 138 \), \( P < 0.001 \), adjusted \( R^2 = 16.2 \)). To examine behaviour during fuelling phases, daily mass gains and intake rates (number of mealworms consumed per hour) were calculated in addition to hourly FDRs (see above) for each day that a bird was present.

Accurate estimation of departure load depends on a bird departing on the evening after which it no longer attended a feeder. Sedge warblers made a mean of 8.9 visits (SD = 3.7, min = 3.2, max = 16) during 2 h of filming on their last day. Given this rate of visitation, there is a very low probability of a bird being present and not being recorded the following day (\( P = 0.006 \), if visitation rate is modelled as a normal distribution). To determine whether birds underwent ‘extensive’ fuelling, it is necessary to define ‘extensive’. Here, a bird capable of completing a nonstop flight from PVR to the Sahel of West Africa (approximately 3800–4200 km), which requires a body mass > 19.75 g (equivalent departure load = 99%), is considered to have fuelled extensively and is termed EX. A nonextensively fuelling bird is termed NEX. Flight ranges were estimated using Flight 1.15 (Pennycook & Battleley 2003) using the following assumptions/values: still air; 85% of any mass increase above LBM consisted of fat; wing span = 0.183 m (mean of 12 measurements from juveniles at PVR); aspect ratio = 5.27 (mean of five birds at PVR); otherwise default values were used.

Estimating Fuelling Durations

‘Raw’ fuelling duration was calculated as the number of days a bird was present at a feeder, except in two cases for which it was the number of days since the start of fuelling (see above). On arrival at a feeder, several individuals were >1 g heavier than the mean mass of sedge warblers captured in mist nets at PVR in 2005 (mean = 10.8 g, \( N = 4682 \), suggesting that fuelling had commenced prior to finding a feeder. To take this into account, an extended duration was calculated as an average of two extrapolated durations: these involved estimating how many days a bird may already have fuelled for if: (1) its FDR was the same as when at a feeder; (2) its FDR was that of ‘natural’ birds (5.3% LBM/day) and it had begun fuelling at a mass of 11 g. ‘Natural’ FDR was the mean for retrapped birds at PVR in 2005 that gained mass and whose FDR was in the top 25% (chosen to exclude nonfuelling birds).

Optimal Migration Models

Predictions for a time-minimizing model were generated using the information in Hedenström & Alerstam (1997). A constant FDR between stopovers, an infinite migratory distance, and variation in FDR being interpreted as ‘global’ variation, were assumed. The assumption that there is a time and energy cost to initiating a stopover is central to the formulation of the model. The model predicts the optimal number of days to spend at a stopover site (written as \( t^* \)), for a given FDR (\( k \)), and varies with the values entered for the stopover cost in time (\( t_0 \)) and energy (\( E_0 \)). Optimal departure loads (\( f^* \)) were calculated by multiplying \( t^* \) by the FDR (\( k \)). An additional time-minimizing model in which migratory distance is finite and FDR is expected to decrease along the migratory route is illustrated in Fig. 2. This model’s predictions were not generated but modified from Fig. 3 of Weber & Houston (1997).

Weather Data

The Meteorological Office provided hourly recordings of wind strength/direction, precipitation and air pressure at sea level from Herstmonceux (50°89’N, 00°32’E, altitude 52 m), approximately 25 km from PVR, for the years 2001–2003. For 2005, data from a weather station at PVR were used. Birds were expected to depart 2 h after sunset (Åkesson et al. 2001) and conditions closest to this time were used. Assuming a preferred migratory direction of 225° (approximate mean direction of sedge warbler movements from the U.K.; Wernham et al. 2002) wind direction and strength were converted into a wind component using Fransson’s (1998) methods. Positive wind components relate to tailwinds, negative to headwinds and zeros to crosswinds.

To examine departures in relation to wind, chi-square tests used expected values based on the frequency of different wind types/components. Two frequency distributions were generated for this purpose: (1) including all days on which birds were present at feeders, on the assumption that birds could leave at any time; (2) including only those days when individual birds were considered ‘ready’ to depart. The criteria for determining ‘readiness’ differed between groups: NEX: all days a bird was present plus the day after departure; EX: all days after
and including day 7 since fuelling began plus the day after departure (no EX birds departed before day 8). Using these periods of readiness, a probability of occurrence was assigned to the conditions on each day based on their periods of readiness, a probability of occurrence was assigned to the conditions on each day based on their

These probabilities were summed across birds to give the final expected frequencies.

Statistical Analyses

EX and NEX birds were compared using two-tailed t tests, while a binary logistic regression was used to investigate the factors influencing fuelling behaviour. Predictions from optimality models regarding the relationship between FDR and departure load/fuelling duration were tested using regression models. A nested ANOVA was used to examine day-to-day variation in fuelling variables within the population and individuals. In no cases were the assumptions of the parametric tests described above broken (Field 2000).

RESULTS

During four autumn migrations, 22 juvenile and two adult sedge warblers attended feeders at PVR, 10 of which (nine juveniles and one adult) fuelled extensively (Fig. 3; departure load > 99%). EX birds had larger departure loads and longer fuelling durations than NEX birds (t tests: departure load: $t_{21} = 10.05, P < 0.001$; fuelling duration: $t_{21} = 9.67, P < 0.001$; Fig. 3). Overall FDRs were generally lower in EX birds but not significantly ($t$ test: $t_{19} = -1.49, P = 0.152$). Conversely, initial FDRs were higher in EX birds ($t$ test: $t_{19} = 3.71, P < 0.001$; Fig. 2). No apparent difference in the date when fuelling commenced was found between NEX and EX birds ($t$ test: $t_{19} = 1.24, P = 0.230$). The extended stays and initial nonfuelling behaviour of one adult and one juvenile were indicative of premigratory fuelling while all other birds could have been on stopover. Notably this adult bird was observed feeding the juvenile and while the juvenile fuelled extensively the adult did not.

A binary logistic regression including initial FDR and ‘start date’ found that higher initial FDRs and later ‘start dates’ increased the likelihood of extensive fuelling, although only the former was significant (logistic regression: $P = 0.032$ and 0.061, respectively). When initial FDR is plotted against start date, only one EX individual overlaps in the two-dimensional spaces occupied by EX and NEX birds (see Fig. 4). This bird may be better classified as NEX, as its departure load only just qualifies as EX (99.9% LBM) and examination of Fig. 6 (bird fuelling between 17 and 24 August 2003) suggests that its fuel load may have been elevated through delayed departure associated with adverse winds between 18 and 23 August. A second logistic regression including the terms initial FDR, ‘start date’ and ‘adverse winds between 18 and 23 August’ was also tested using regression models. A nested ANOVA was used to examine day-to-day variation in fuelling variables within the population and individuals. In no cases were the assumptions of the parametric tests described above broken (Field 2000).

Optimization of Fuelling Behaviour

Energy/time-minimizing models predict that departure load will increase smoothly with FDR if migratory distance...
fuelling durations in relation to initial FDR suggests that the durations of NEX and EX birds form two separate steps (in a similar fashion to the relationship between departure load and initial FDR in Fig. 2).

**Variation in Fuelling Rate Between Days**

One assumption of Hedenström & Alerstam’s (1997) time-minimizing model is that FDR is constant throughout a fuelling period. At the population level, both hourly FDR and daily mass gain decreased as departure approached (Fig. 5; regression: hourly FDR: $F_{1,55} = 16.33$, $P < 0.001$, adjusted $R^2 = 21.5\%$; daily mass gain: $H_1 = 17.1$, $P = 0.004$), a relationship whose significance held when individual birds were nested within ‘day relative to departure’ (ANOVA: hourly FDR: $F_{10,21} = 7.18$, $P < 0.001$; daily mass gain: $F_{2,16} = 5.11$, $P = 0.003$). Intake rate (mealworms/hour) showed no trend with day relative to departure (Fig. 5; nested ANOVA: intake rate: $F_{17,41} = 0.67$, $P = 0.812$).

**Departure Decisions and Weather**

Of the 24 sedge warblers, eight departed with headwinds, one with a crosswind and 15 with tailwinds. Departures in relation to wind component, which reflects both wind direction and strength, can be seen in Fig. 6. On no occasion did birds depart on nights with rain or when rain had fallen in the 6 h prior to departure. Air pressure was higher on nights with departures relative to nights without ($t$ test: $t_{40} = 2.30$, $P = 0.027$). Relative to the frequency of head/cross winds and tailwinds whilst birds were present at feeders (see Methods, distribution A), birds departed with tailwinds more often than would be expected by chance (chi-square test: $\chi^2_1 = 4.92$, $P = 0.027$). However, if birds are treated individually and are considered ready to depart only on certain days (see Methods, distribution B), conditions at departure were not significantly different from those expected by chance (chi-square test: $\chi^2_1 = 0.555$, $P = 0.456$); although the greatest difference between observed and expected values was for EX birds departing in tailwinds.

That sedge warblers do not appear to actively choose tailwinds is surprising, however, this may be because light cross/headwinds have little impact on flight range. Indeed, six birds departed in cross/headwinds of $\leq 3.6$ km/h and only three birds departed in stronger winds. To examine whether birds were avoiding stronger headwinds, the expected frequency of wind components on nights when birds were ‘ready’ to depart was calculated (see Methods). However, the observed pattern of wind components on departure nights could still have occurred by chance (chi-square test: $\chi^2_1 = 4.0$, $P = 0.261$). Some of the departures in headwinds by EX birds might be explained by extensive delays forcing birds to depart whatever the conditions. This may be true of the bird that began fuelling on 16 August 2005 (see Fig. 6).
DISCUSSION

Dual Fuelling Behaviours

Given access to the same resources, migrants might be expected to adopt the same fuelling behaviour and therefore migratory strategy, assuming there is little variation in the ability to use those resources. In this study, sedge warblers had access to a clumped, superabundant food supply, which was believed to be the cue for extensive fuelling, however, only 10 out of 24 birds did so. Indeed, it was evident that two distinct fuelling behaviours had been adopted. One set of birds (NEX) remained for a mean of 3.7 days and accumulated a limited amount of fuel while the second set (EX) fuelled for a mean of 11.6 days and gained sufficient fuel for a nonstop flight from the U.K. to sub-Saharan Africa (Fig. 3). The ability to utilize the available resources did differ between groups, as reflected by significantly higher initial FDRs in EX birds, however, initial FDRs were not mutually exclusive between groups, showing considerable overlap (Fig. 2). Food availability is therefore unlikely to be the sole determinant of whether birds fuelled extensively. Indeed, the threshold FDR above which extensive fuelling occurred (>13% LBM/day; Fig. 3) is rarely attained under natural conditions: max FDR = 12% LBM/day in Bibby et al. (1976).

Temporal and geographical cues are plausible additional determinants of fuelling behaviour, given that the temporal abundance of aphids varies on a geographical scale. Phragmites reeds mature and senesce earlier in the year as mean summer temperature increases, giving rise to a north–south cline within Western Europe and the timing of reed aphid abundance reflects this cline (Bibby & Green 1981). The optimal region for seeking an abundance of aphids will therefore depend on time of year: early migrating birds might be expected to use more southerly sites (which have the added benefit of reducing fuel load requirements) while later migrants should use increasingly northerly locations (e.g. PVR). The results presented here partly agree with this prediction, as mean ‘start’ date for EX birds was later than NEX birds but not significantly so (a larger sample size may clarify this).

This nonsignificant result might be explained if extensive fuelling at PVR is favourable for early migrants when a threshold FDR is attained. Given the temporal and geographical distribution of aphids, early migrants at PVR would be expected to stop briefly before heading south to where aphid abundance is peaking, unless a threshold FDR is exceeded, cancelling out the cost of a greater migratory distance. This threshold is expected to decrease with date in line with a decline in aphid abundance at sites south of PVR. Initial FDR did decrease with ‘start date’ in EX birds if one individual was reclassified (see Results and Fig. 4 for reasoning), potentially reflecting this decreasing threshold. Indeed, using the same reclassification, a logistic regression including the interaction between initial FDR and start date was a ‘perfect predictor’ of whether birds fuelled extensively.

Considered alongside the distribution of NEX and EX birds in Fig. 4, these results suggest that in early August all birds stop briefly at PVR, as southerly sites are optimal
for fuelling, while in mid-August, the threshold for switching behaviours is lower and birds with high initial FDRs remain to fuel extensively. By late August, the threshold drops further and most birds fuel extensively. This is supported by Bibby et al.’s (1976) finding that later migrating sedge warblers in the U.K. have larger reserves. Sedge warbler fuelling behaviour may therefore have evolved in a remarkable way to respond to the temporal and geographical distribution of aphid abundance.

**Optimization of Fuelling Behaviour**

The brief period in which aphids are superabundant in northwest European reedbeds (Bibby & Green 1981) suggests that time-minimization should be a key selective pressure on autumn migrating sedge warblers. Furthermore, sedge warblers breeding in northwest Europe moult in the Sahel region of West Africa (Morel & Morel 1992; Wernham et al. 2002), where invertebrate abundance is determined by the erratic wet season between June and October. Therefore, early arrival in this region may be advantageous in order to finish mouling before the onset of the dry season (Bensch et al. 1991).

Time-minimizing models predict a positive relationship between FDR and departure load (Alerstam & Lindström 1990). This was not true of sedge warblers at PVR when overall FDR was considered but was for initial FDR. This departure from the models, when considering overall FDR, arises from the violation of the underlying model assumption that FDR remains constant throughout the fuelling period (Hedenström & Alerstam 1997; Weber & Houston 1997). This assumption is broken by EX birds, in particular, whose FDR gradually decreases in the later stages of fuelling (see Figs 5 and 6). Rising metabolic demands associated with the maintenance and transport of an increasing fuel load are most probably the cause of this decrease (Klaassen & Lindström 1996). Reed warblers seem to compensate for similar rising energy demands by increasing their intake rate, which may otherwise be reduced to minimize foraging-intensity dependent predation risk (Bayly 2006). There is no evidence that sedge warblers do the same (Fig. 5), implying that sedge warblers are already foraging at maximum rates; as expected of a strongly time-selected migrant (Alerstam & Lindström 1990).

It is apparent that a time-minimizing model in which migratory distance is considered finite, giving rise to
a stepped function, provides a good qualitative fit to the data on sedge warblers (Fig. 2). Nevertheless, both finite and infinite distance models can give rise to the observed duality in fuelling behaviour. In a finite model, the optimal solution is to divide the journey into equal stages where each step in the resulting stepped function represents a decrease in the number of stages (Weber & Houston 1997; Fig. 2). If the expectation of FDR at future sites is lowered, these steps become shorter and the switch between steps occurs at lower FDRs. For early migrants at PVR, aphid abundance and therefore FDR are expected to be higher at future sites, while the opposite is true of later birds. The finite model therefore predicts that few early migrants will fuel extensively while later birds are more likely to, as the step occurs at a lower FDR. The data presented here are in agreement with this prediction and there is even an overlap in the FDRs of EX and NEX birds as would be expected (Fig. 2). When distance is considered infinite (smooth function) two models are needed, the first resulting from an expectation of increasing resources ahead (NEX birds) and the second from an expectation of decreasing resources (EX birds). These two models predict that EX and NEX birds will have very different departure loads but departure load should still increase with FDR within groups (Fig. 2). There is some evidence for these increases but the case is not clear-cut. Regardless of which model sedge warblers conform to, they point to the evolution of an innate perception of future conditions as being a highly plausible mechanism for explaining the observed duality in fuelling behaviour.

**Departure Decisions and Weather**

While sedge warblers appeared to avoid departing in rain or high winds, their departures were not as closely related to tailwinds as might be expected (Liechti & Bruderer 1998). This may be due to light head/crosswinds being considered suitable for departure, which is not unexpected given that a light wind will have little negative impact on potential flight range; especially for NEX birds which are likely to be making relatively short flights. Alternatively, birds may be finding favourable winds at higher altitudes, which can differ from those recorded at ground level (Schaub et al. 2004). However, for EX birds that must manage their fuel effectively to reach sub-Saharan Africa, this result is surprising. The greatest contributors to the chi-square analyses suggest that EX birds were more likely to chose tailwinds and avoid strong headwinds but not significantly so. This apparent insensitivity to wind conditions may have resulted from a small sample size, combined with some individuals departing regardless of conditions due to long delays (Weber et al. 1998). However, it may also be argued that migrants making long flights have reduced sensitivity to initial conditions.

**Sedge Warblers versus Reed Warblers**

A comparison of the relationship between FDR and departure load for sedge (data presented here) and reed warblers (taken from Bayly 2006) attracted to mealworms at PVR highlights a number of differences (see Fig. 7). For example, FDRs are higher in sedge warblers, which may be achieved by reducing predator awareness and increasing feeding rates and/or through physiological adaptations such as increased gut size. It also shows the fuel loads of reed warblers falling half way between those of EX and NEX birds. If NEX birds have an expectation of increasing resources and EX birds a decreasing expectation, then reed warblers may well have a constant expectation. Finally, this comparison further highlights that food availability and therefore FDR is not the only determinant of fuelling behaviour; there are clearly hardwired behaviours that give rise to quite different outcomes under the same conditions: even within ecologically and morphologically similar species.

Other species of long-distance migrants utilize clumped, superabundant resources (e.g. garden warblers, Sylvia borin and fruit) but do not accumulate extensive fuel reserves. Evidently, the close association between sedge warblers and aphid abundances has made this strategy optimal in this species. Ultimately, sedge warblers adopt a high-risk strategy that is dependent on a highly variable food source, both in time and space, and presumably expose themselves to a high level of predation risk by fuelling at maximum intensities and compromising their escape ability by grossly increasing their body mass (Gosler et al. 1995). The success of sedge warbler migration is likely to be as sensitive to the effects of climate change on aphid abundance and phenology, as their overwinter survival is to erratic rainfall in the Sahel (Peach et al. 1991).
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