



Grasshopper Warbler *Locustella naevia* autumn migration – findings from a study in southeast Britain

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This study examines the migratory behaviour of Grasshopper Warblers *Locustella naevia* on the south coast of Britain with respect to phenology, fuel loads, stopover behaviour and potential flight ranges. Data were derived from 5,455 mist-net captures gathered over 10 years between July and October at the Pannel Valley Reserve, East Sussex. For the majority of captures and recaptures, fat score, wing length and body mass were recorded. Data from recaptures were used to calculate fuel deposition rates and stopover durations, whilst fat scores and body masses were used to calculate fuel loads and potential flight ranges. The majority of birds were carrying moderate fuel reserves and very few birds refuelled at the reedbed site; indeed, many appeared to remain at the site for just one day. Estimated flight ranges suggest that most birds were capable of flying to the southern half of France. Therefore it is suggested that British birds typically accumulate fuel north of the south coast, possibly at or close to their breeding grounds, and do not refuel until reaching southern France. This is supported by the pattern of birds recovered abroad. That birds stop at the south coast at all is attributed to the English Channel acting as a barrier to onward flights.

The nominate form of the Common Grasshopper Warbler *Locustella naevia* breeds patchily across a wide belt of northern Europe and the majority of the population is believed to winter in West Africa (Cramp 1992). Whilst populations appear relatively stable in continental Europe, the population in the UK has declined significantly since 1976, although it is believed to have stabilised over the last 10 years (Baillie *et al* 2005). The decline has been attributed to habitat destruction (Gibbons *et al* 1993); however, other factors have not been ruled out. As a long-distance migrant, the Grasshopper Warbler may be particularly sensitive to changes in habitat quality on a large geographic scale. Migration is an energetically demanding behaviour and migrants require sites with sufficient resources to facilitate the accumulation of fuel for migratory flights (Alerstam & Hedenström 1998). Most migrants are unable to accumulate enough fuel to fly directly from their breeding to wintering grounds, making them reliant on 'stopover' sites for refuelling. Changes at stopover sites can dramatically affect the success of migration and thus it is important to identify the migratory strategy and the stopover sites used by Grasshopper Warblers, if their decline is to be fully understood (Weber *et al* 1999).

Currently, the migratory behaviour of Grasshopper Warblers is poorly known and Cramp (1992) suggested that the scarcity of records, even in well-studied areas, was due to birds making long unbroken flights. Alternatively the Grasshopper Warbler's preference for dense vegetation,

like reedbeds, where it is hard to detect, may be responsible. Despite many ringing studies in Britain having focused on reedbeds, the majority have recorded low capture rates (Wernham *et al* 2002). In a study of fat loads in carcasses collected at Bardsey lighthouse, Baggott (1986) found that, in comparison with Sedge Warblers *Acrocephalus schoenobaenus*, Whitethroats *Sylvia communis* and Willow Warblers *Phylloscopus trochilus*, Grasshopper Warblers carried the largest fat loads, and estimated that birds were capable of a non-stop flight to southwest France. Southwest France is the location for all three autumn recoveries of British Grasshopper Warblers in continental Europe up to 1998 (Wernham *et al* 2002).

Here we present the results of a ringing study in southeast Britain where significant catches of Grasshopper Warblers were made annually between 1995 and 2004. To address the current lack of information on Grasshopper Warbler migration, data are presented on the phenology of migration, the degree of fat storage in passage birds, the duration of stopovers and the accumulation of fuel reserves in birds stopping over. Estimated fuel stores are used in conjunction with estimates of flight range to predict where birds leaving the site are likely to refuel. Finally, the movements of birds caught away from their site of ringing are used in conjunction with estimates of flight range to suggest where important stopover areas may lie and to elucidate the migratory strategy of the Grasshopper Warbler.

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METHODS

Study site

The Pannel Valley Reserve (PVR), southeast England (50°54'N 0°41'E), consisted of a 23 ha mosaic of reedbed, *Salix* scrub and open water, surrounded by mixed farmland and grazing marshes, 1.7 km from the English Channel coast. Since 1986, approximately 30,000 migrating birds have been captured in mist nets each autumn at PVR by staff of the Wetland Trust and a large number of volunteer ringers. Nets were located in reedbed (largely pure stands of *Phragmites*), *Salix* scrub and an area of elder and bramble, with 700–800 m of net typically being deployed.

Data collection

Permanently erected mist nets were opened daily between July and the end of October, unless weather conditions prevented this. Nets were opened 0.5 hours before sunrise and were open for an average of 6.1 hours per day ($n = 1,013$, $sd = 1.93$, range = 0.75–14). The nets were set just 15 cm above the ground in order to increase captures of low-flying Grasshopper Warblers (Rumsey 1975). The length of operational nets on a given day depended on the number of ringers present and wind strength (reedbed nets only; $n = 1,013$, mean = 470 m, $sd = 157$, range = 102–699). These methods resulted in 5,455 captures of Grasshopper Warbler between 1995 and 2004.

Grasshopper Warblers trapped in mist nets were processed as quickly as possible and the following data were recorded: date; time of capture as hour of extraction; age as determined using the criteria laid out by Svensson (1992); wing length, measured to the nearest 1 mm using the maximum chord method (Svensson 1992); body mass, measured to nearest 0.1 g using either a Pesola or electronic balance; fat deposits, scored on a nine-point scale, ranging between 0 and 8 (Kaiser 1993).

Sound lures

The song of Grasshopper Warbler, amongst other species, was played through one to three speakers located approximately a metre away from nets within the reedbed, throughout the main migration period of this species (mid July to end September). Near-continuous playback of Grasshopper Warbler song at a volume a little above that of natural song commenced one hour before dawn and continued until net closure (typically 1000 GMT). Sound-lure use may affect the natural behaviour of migrants, thereby making the interpretation of resulting data problematic (Schaub *et al* 1999). To address this issue, the body mass, fat scores, wing length and stopover behaviour of a set of 137 birds that were captured without sound lures at PVR were compared to sound-lured birds. Sound lures were not used on these days either because

they were outside the main Grasshopper Warbler migration period or as a result of electrical failure. In addition, capture data for 232 Grasshopper Warblers from 13 different UK south-coast sites that did not use sound lures were obtained from the British Trust for Ornithology (BTO) to provide a further comparison with the sound-lured birds.

Phenology analysis

Several variables may influence capture rate on a given day, the most important being time of year and trapping effort both in terms of net length and hours of operation. In addition, variation in sound-lure use and weather are likely to influence captures. During this study, trapping effort and sound-lure use were kept as constant as possible, although occasionally either weather or manpower limited trapping effort. Initial analyses indicated that relationships between these variables were very complex and attempts at correcting the data gave rise to extreme data points. The correlation between poor weather, low migratory activity and reduced trapping effort is responsible for many of these difficulties. To avoid inappropriate corrections, days with reduced trapping effort were removed from the data set based on two threshold levels: net length <345 m (reedbed nets or those close to speakers playing Grasshopper Warbler song would be closed below this level) and nets open for less than 4.5 hours (>90% of captures took place within the first 4.5 hours: *eg* analysis of capture data from 27 days on which more than 10 individuals were captured (cumulative percentage of captures by hour after sunrise) – hour 1 (60%); 2 (73%); 3 (82%); 4 (88%); 5 (93%); 6 (97%)). A generalised linear model (GLM) was employed to test whether either aspect of trapping effort still affected capture rates in the reduced data set (see results). The final phenology was generated by taking three-day averages of daily capture totals for the 10 years considered (see Fig 1).

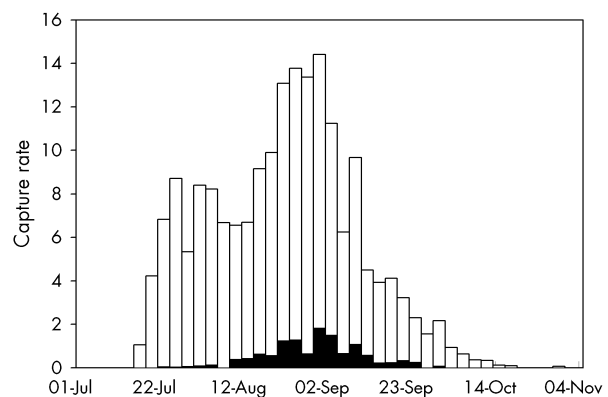


Figure 1. Timing of autumn passage of juvenile (white) and adult (black) Grasshopper Warblers through the Pannel Valley Reserve. Daily capture rates were averaged over 10 years using a reduced data set (see Methods) and are presented as three-day averages.

The phenology of adult birds was estimated by working out the fraction of adults in daily catches and multiplying the appropriate mean fraction by the three-day averages calculated above.

Body mass, fat scores and lean body mass

Body mass varied with time of day: therefore the body mass of all captures were corrected to the median time of capture (relative to sunrise) using the coefficient from a GLM controlling for wing length (hour relative to sunrise, ANOVA: $F_{2,4481} = 65.8$, $P < 0.001$, coefficient = 0.097 g/h). The resulting corrected masses are used in all aspects of this study unless otherwise stated. Fat scores were analysed without correction. Size-specific lean body mass (LBM) was estimated from a GLM containing the body mass of birds with a fat score of zero and the variables 'wing length' and 'age'.

Fuel loads, body mass changes and fuel deposition rates

Body mass changes, which reflect changes in fuel stores (Redfern *et al* 2004), were calculated as the change in mass between captures. Fuel load and fuel deposition rate (FDR) were quantified as a percentage of a bird's size-specific LBM, to take into account differences in overall structural size between individuals. Fuel load will thus be expressed as a percentage of LBM, and FDR as the percentage of LBM accumulated per day. FDR could only be calculated for birds trapped on two separate occasions. As capture events are believed to result in mass reductions (Gosler 2001), only maximum FDRs were calculated, to minimise these effects. To quantify maximum FDRs from data on mist-netted birds, the maximum observed rate of mass increase was calculated between successive captures of each retrapped bird (for birds captured twice this was simply the rate between first and last captures).

Stopover durations

Minimum stopover durations were calculated as the time elapsed between first and last captures (Morris *et al* 2005), although, to increase comparability between methods, annual means also included individuals trapped only once. In addition, stopover analyses were run by the Computational Ecology Research Group at Canisius College, Buffalo, New York, using open population models and multiple-day constancy intervals following Morris *et al* (2005, 2006). 'Multiple-day constancy' models, which avoid pooling-induced errors, were used to generate two estimates: 1) 'Stopover After' (Morris *et al* 2006) – a weighted stopover duration for the period after first capture, equivalent to equation 5 in Efford (2005), and 2) 'Total Stopover' – a weighted duration for the period both before and after first capture, equivalent to that proposed

by Schaub *et al* (2002). Considerable debate surrounds the estimation of stopover duration (see Efford 2005): here we favour estimates for the period after first capture ('Stopover After') both on mathematical grounds (Efford 2005) and because they are more appropriate to the situation at PVR (sound-lure use and the number of mist-nets deployed are expected to give rise to a high probability of capture on first arrival).

Flight ranges

Flight ranges were calculated using version 1.15 of Pennycuick's Flight program (accessed 31 March 2005, www.bio.bris.ac.uk/people/staff.cfm?key=95; Pennycuick & Battley 2003). Birds were modelled with a wingspan of 0.179 m (mean of 20 autumn measurements; Baggott 1986), an aspect ratio of 5.27 (Pennycuick states that the aspect ratio of similar species is appropriate; here, mean of five personally measured Sedge Warblers = 5.27 and Pennycuick's wings database gives 5.26 for Marsh Warblers) and a flight altitude of 500 m (varying flight altitude has little effect on estimates). The default setting of 0.17 was used for the flight muscle fraction. 'Fat mass' was calculated by subtracting the LBM of a bird of mean wing length (11.75 g) from the 'empty body mass' and taking 85% of that figure. Thus 85% of any increase above LBM is expected to be fat whilst protein combined with water makes up the rest (Piersma 1990). Actual fat content may be higher, given that Baggott (1986) found that fat accounted for 100% of increases above the mean LBM of 11.55 g for juvenile birds ($n = 20$). Default settings were used for all other inputs. Flight ranges were calculated for birds of mean mass and at either quartile of the population using two sets of body mass: 1) uncorrected (see above) body mass of all new captures; 2) estimated evening body mass – calculated using corrected body mass on the conservative assumption that birds gained mass for only six hours between dawn and dusk at the rate estimated for the whole population (0.097 g/h; see above).

Movements

Details of all ring recoveries from Grasshopper Warblers ringed in Britain & Ireland for the period up to 2004 were obtained from the BTO (43 records). The movements of birds recovered during the main autumn migration period (July–November) that had moved further than 30 km (17 records) were mapped using the distribution mapping program DMAP (Alan Morton, Windsor; www.dmap.co.uk).

Statistical analysis

Three main parametric statistics, t-tests, regression and generalised linear models, and the non-parametric test, Mann–Whitney, were calculated using Minitab release 13.3

and in no cases were the assumptions of these methods invalidated (Field 2000).

RESULTS

Sound lures

No difference in wing length was found between non-sound lured (NSL) and sound-lured (SL) birds at PVR (t-test, $t_{124} = -1.17$, $P = 0.25$), however NSL birds did have higher fat scores (Mann-Whitney, $n = 122$, $W = 276,703$, $P = 0.003$). Body mass was significantly higher in NSL than SL birds at PVR in a GLM model correcting for wing length, date and age ('Sound', ANOVA, $F_{1,4339} = 13.6$, $P < 0.001$), although the difference was small: mean difference in body mass with 95% CI = 0.35 ± 0.19 g. Minimum stopover durations at PVR were not significantly different between NSL and SL birds (Mann-Whitney $n = 136$, $W = 356,431$, $P = 0.81$): indeed 92.7% of NSL and 92.5% of SL birds were captured just once. This non-significant result held when only including birds for which sound lures were not in use for three clear days after initial capture and excluding birds caught only once (Mann-Whitney, $W = 254,584$, $P = 0.81$).

NSL birds from other south-coast sites were also significantly heavier than SL birds at PVR but less so ('Sound', ANOVA, $F_{1,4448} = 6.63$, $P = 0.010$; mean mass difference \pm 95% CI = 0.18 ± 0.07 g), whilst no difference was found in fat scores (Mann-Whitney, $n = 60$, $W = 116,115$, $P = 0.982$). Retrap records for NSL birds away from PVR were insufficient for examination of stopover duration.

Phenology

A GLM analysis of a reduced data set of daily capture totals revealed that 'net length' did not significantly affect capture totals (ANOVA, $F_{1,779} = 0.21$, $P = 0.645$). 'Net hours' was marginally significant in the same model but a correction would make little difference to the final phenology due to a small coefficient (ANOVA, $F_{1,779} = 4.07$, $P = 0.044$, coefficient = 0.27). The phenology resulting from the reduced data set (Fig 1) indicates that Grasshopper Warbler passage began in mid July, and went through two main peaks, before winding down in late September/early October. It also shows juveniles commencing their migration before adults (Mann-Whitney, $P < 0.001$).

Body mass, fat scores and lean body mass

Adult birds were slightly heavier than juveniles (t-test, variances not pooled: $t_{353} = 4.30$, $P < 0.001$, estimate of difference = 0.24 g; mean \pm sd, adult 13.06 ± 1.02 g, juvenile 12.96 ± 0.92 g; see Fig 2a) and birds that were later retrapped had lower body mass on first capture than those that were not (t-test, variances pooled: body mass, $t_{4799} = -8.64$, $P < 0.001$). Body mass decreased with date

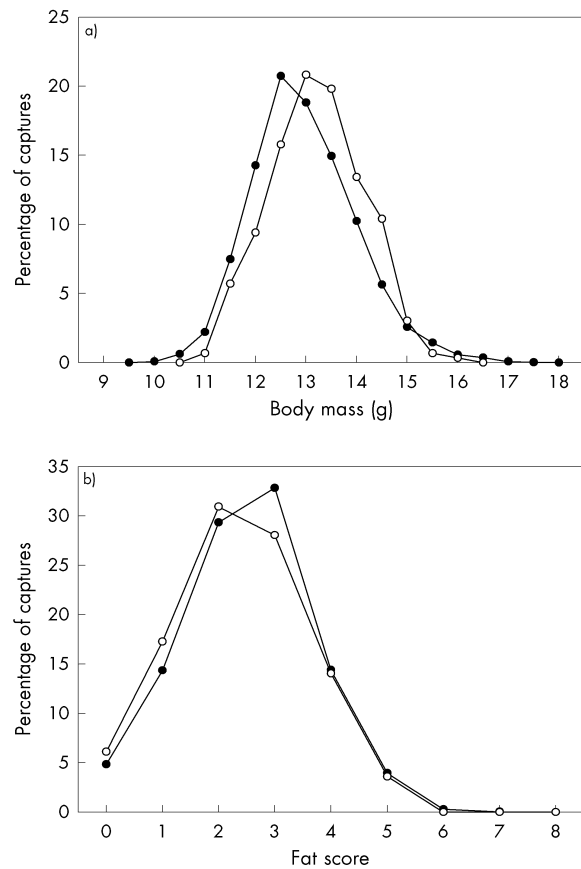


Figure 2. Distribution of a) corrected body masses and b) fat scores (Kaiser 1993) of autumn-migrating juvenile (black circles) and adult (white circles) Grasshopper Warblers captured at PVR.

but the effect size was extremely small at just 0.002g/day (regression: $F_{1,4391} = 5.43$, $P < 0.001$, adjusted $R^2 = 0.1\%$). The majority of birds trapped were carrying visible fat deposits (Fig 2b; mean and median fat scores = 2.5 and 3 respectively) and juveniles averaged slightly higher fat scores than adults but the difference was not significant (Mann-Whitney, $P = 0.071$).

A GLM model gave rise to the following equation for estimation of lean body mass: $LBM = 3.90 + 0.13 \times \text{Wing Length} \pm 0.35$ (+ adult, - juvenile: ANOVA, Wing, $F_{2,202} = 16.2$, $P < 0.001$; Age, $F_{2,202} = 15.9$, $P < 0.001$). The estimated LBM for a juvenile of mean wing length (11.87 g, 64 mm) is similar to that of juvenile Grasshopper Warbler carcasses from which the fat has been extracted (mean = 11.55 g, $n = 20$, wing lengths not stated; Baggott 1986).

Fuel loads, body mass changes and fuel deposition rates

Fuel loads, described as a percentage of LBM, were larger in juveniles than adults: juvenile, $n = 4,046$, mean \pm sd = $10.6 \pm 8.1\%$ /LBM, max = 47.3; adult, $n = 293$, mean \pm sd = $8.0 \pm 6.4\%$ /LBM, max = 28.3 (Mann-Whitney, $P < 0.001$).

Table 1. Comparison of Stopover Duration estimates (mean \pm sd) by year using three different methods: A) minimum stopover duration; B) 'Stopover After' durations estimated from multiple-day constancy models; C) 'Total Stopover' durations estimated from multiple-day constancy models. All estimates are given in days. Years 1997 and 2001 are omitted as no suitable model could be found to fit the data.

	1995	1996	1998	1999	2000	2002	2003	2004
A	1.25 \pm 0.94	1.30 \pm 1.43	1.18 \pm 0.94	1.20 \pm 0.89	1.21 \pm 1.05	1.30 \pm 1.21	1.27 \pm 1.39	1.23 \pm 1.18
B	1.35 \pm 0.25	1.75 \pm 0.41	1.83 \pm 1.06	2.10 \pm 1.04	1.90 \pm 1.44	1.73 \pm 0.38	1.58 \pm 0.47	2.13 \pm 1.02
C	2.59 \pm 0.46	3.65 \pm 2.73	3.58 \pm 1.92	3.94 \pm 1.76	3.59 \pm 3.64	3.36 \pm 1.03	3.08 \pm 0.84	3.90 \pm 1.63

Of 4,949 birds ringed, only 429 were retrapped and body mass changes, which were largely negative (Fig 3), could be calculated for only 298 of these. Body mass changes between captures were negatively related to body mass on first capture (regression: $F_{1,296} = 39.1$, $P < 0.001$, adjusted $R^2 = 11.4\%$), whilst the time between captures had no apparent effect (Regression: $F_{1,296} = 0.11$, $P = 0.741$).

Despite FDRs being calculated to give maximum rates many were still negative (mean \pm sd = $-1.25 \pm 3.77\%$ LBM/day). FDRs were more likely to be positive the longer a bird remained at PVR (Regression: $F_{1,296} = 14.3$, $P = 0.001$, adjusted $R^2 = 3.2\%$), a pattern that was demonstrated in birds staying for periods greater than five days (see Fig 4). FDRs showed no relationship with date (Regression: $F_{1,296} = 0.17$, $P = 0.684$). Twelve birds were retrapped the same day as their initial capture but not subsequently: over a period of < 4 hours, six gained mass, two showed no change and four lost mass. The mean rate of positive gain ($n = 6$, 0.125 g/h) was slightly higher than the estimated increase in body mass per hour (0.097 g/h) for the whole population.

Stopover durations

The majority of birds (91%, 4,551 birds) were captured only once and were probably present at PVR for just one day. Of the 9% (429 birds) that were recaptured, two thirds

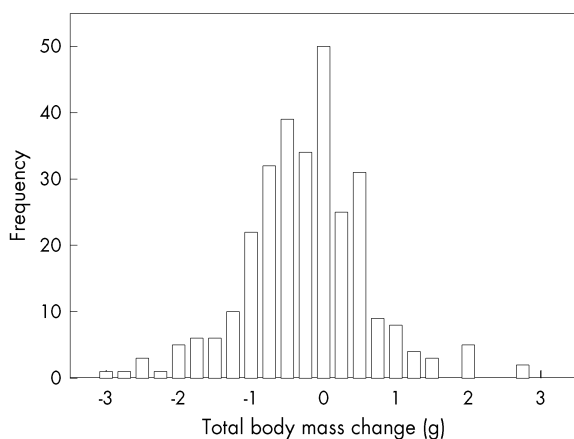


Figure 3. Distribution of body mass changes for 298 Grasshopper Warblers that were retrapped at least one day after their initial capture at PVR.

(282 birds) had a minimum stopover duration of three days or less (Fig 5). Estimated 'Stopover After' durations were also short and showed little variation between years (Table 1). Like Efford (2005), we found that 'Total Stopovers', calculated in accordance with Schaub *et al* (2002), were typically twice as long as 'Stopover After' durations, and had standard deviations that indicated greater variation in duration about the mean (Table 1).

Flight ranges

Body masses and corresponding flight range were estimated for two sets of data: 1) uncorrected body masses and 2) estimated evening body masses (see methods). The following estimates for birds of mean mass and at either quartile of the population are expressed as a range defined by the two sets of body masses: mean body mass, 13.06–13.56 g, 537–747 km; lower quartile, 12.3–12.88 g, 218–460 km; upper quartile, 13.7–14.18 g, 802–1,004 km.

Movements

Five Grasshopper Warblers trapped at PVR occurred at other sites during autumn migration: three in France, one in Britain and one in Ireland (Fig 6). Of note, a 15 g bird in Yorkshire arrived at PVR two days later weighing 12.9 g (distance 382 km) and a 12.4 g bird left PVR and was retrapped in southwest

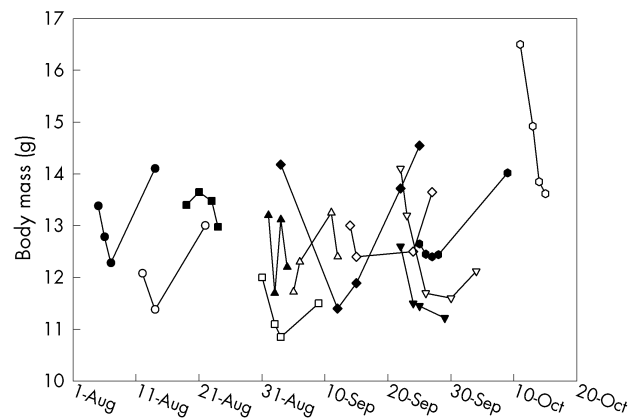


Figure 4. Patterns of change in body mass against date for individual Grasshopper Warblers that were retrapped at least four times during their stay at PVR, between 1995 and 2004. Different symbols are used to assist interpretation of the data.

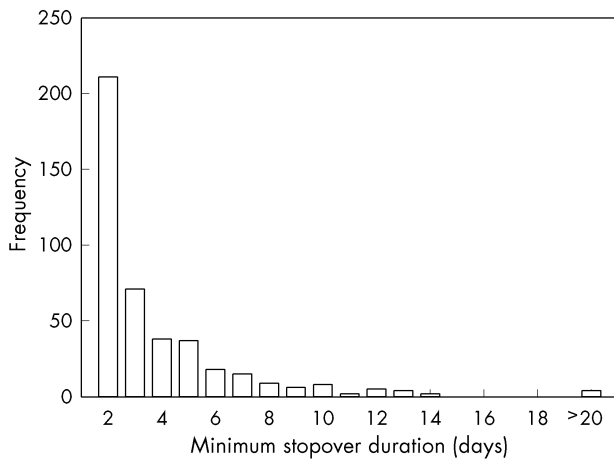


Figure 5. Distribution of minimum stopover durations for 429 Grasshopper Warblers (approximately 9% of the birds captured) retrapped at PVR between 1995 and 2004. Birds trapped only once are not plotted.

France seven days later weighing 13 g (distance 728 km). Movements from elsewhere in Britain include a further two birds found in southwest France (Fig 6).

DISCUSSION

The large numbers of Grasshopper Warblers mist-netted at PVR provide a useful insight into the migratory behaviour of this poorly-known species. The size and utility of this data set is due largely to the use of sound lures and therefore it is important to consider what biases, if any, sound lures may have introduced. Sound lures are known to increase capture rates (Schaub *et al* 1999) and can bias sex ratios (Herremans 1989). Increasing capture rates *per se* will not introduce bias into sound-lured samples; however, Schaub *et al* (1999) found that sound lures played throughout the night can induce landfall, thus altering natural behaviour. At PVR, songs were played from one hour before dawn and therefore are unlikely to have induced landfall of nocturnal migrants. Lures may have influenced the decision of birds looking for somewhere to land but as these birds would have landed anyway, especially given the proximity of the English Channel and the suitability of the habitat at PVR, the trapped birds are still expected to reflect natural behaviour. Indeed, in comparison to two non-sound-lured samples, sound-lured birds differed only slightly in energetic status, and their subsequent stopover behaviour did not appear to differ at all. It is interesting to note that NSL birds had slightly higher body masses than SL birds, which rules out the possibility that only fuel-depleted birds would naturally stop if sound lures were not used. Consequently, we believe that the results presented here reflect, as closely as a mist-netted sample can, the behaviour of Grasshopper Warblers at the south coast of Britain.

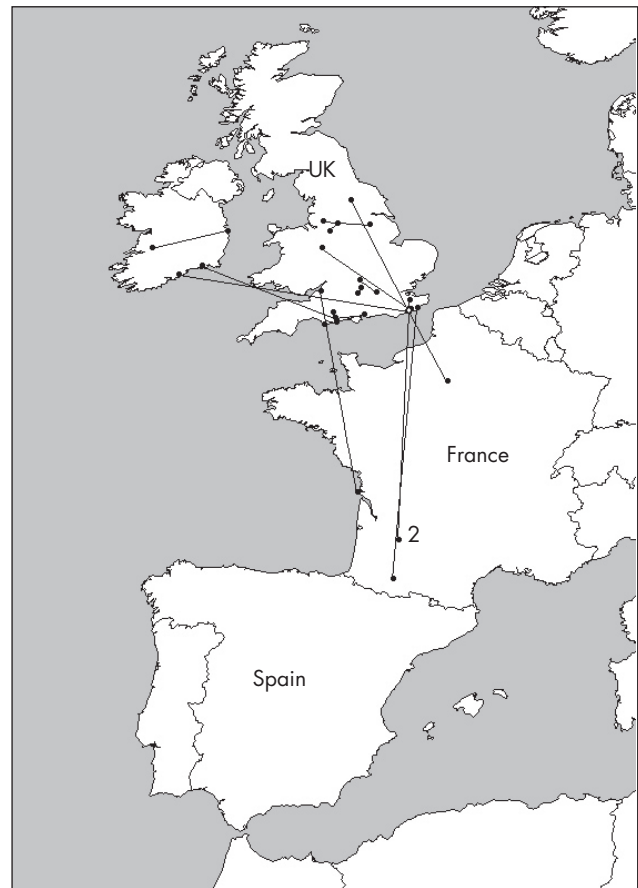


Figure 6. Autumn movements of Grasshopper Warblers ringed in Britain & Ireland. Includes all birds ringed in Britain & Ireland that moved further than 30 km and were recovered between July and November prior to 2005 (data supplied by BTO). Where a movement involves more than one bird, this is indicated with a number. The Pannel Valley Reserve is represented by an unfilled symbol.

Phenology

Grasshopper Warblers began passing through PVR in mid July and showed two peaks in passage, at the end of July and then at the end of August, after which passage tailed off until mid October (Fig 1). The first birds to arrive may have been dispersing juveniles rather than true migrants; however, body mass was highest in these birds, so that energetically these birds appear to be active migrants. Further, PVR is not close to the recent breeding strongholds of Grasshopper Warblers (Gibbons *et al* 1993) and is unlikely to receive dispersing birds. The peaks in passage are thought to represent the progression of first and second broods through the site: a third variable peak in late September (visible in individual years) was lost in the averaging process but probably equates to a highly variable third brood. A similar pattern for different broods is described by Glue (1990) and Wernham *et al* (2002).

Adults began migrating later than juveniles and unlike other Sylviidae of which the same is true, *eg* the

Whitethroat (Cramp 1992), later passage is not caused by adults undergoing a complete post-breeding moult. Adult Grasshopper Warblers have a partial post-breeding moult; therefore, its later migration is better explained by the majority of the population attempting a second or even third brood (Glue 1990).

Fuel for migration

Birds arriving at PVR were already carrying moderate fat reserves (Fig 2) and must therefore have fuelled to the north of the site. Given the relatively short distance between breeding areas in the UK and PVR (50–600 km; assessed from Gibbons *et al* 1993), it would appear likely that birds fuelled at or near to their breeding sites. The body mass of adult birds was slightly higher than juveniles (Fig 2) but because their LBM was also higher, they were actually found to be carrying less fat than juveniles. Baggott (1986) also found that adults had higher LBMs and smaller fat reserves but that body masses were lower not higher. What gives rise to higher LBMs in adults is unclear. Relative to the mean autumn body mass reported from Bardsey, North Wales (Baggott 1986), the mean mass at PVR was significantly lower (mean \pm sd for juveniles only: PVR = 13.04 ± 1.03 ; Bardsey 14.08 ± 0.29 ; one sample t-test, test mean = 14.08, $t_{4094} = -64.5$, $P < 0.001$), which is presumably due to birds having used a greater mass of fuel to reach a more southerly site. The range of body masses from mist-netting studies across Europe is similar to the range recorded at PVR, although heavier birds were recorded at Helgoland, Germany, and in the Camargue, France (Cramp 1992). Given the energetic status of birds at PVR, it is unlikely that they would routinely stop over at the site to increase their reserves.

Stopover behaviour

The majority of birds (91%) trapped at PVR were not subsequently retrapped, suggesting that most birds only paused their migration there between successive nocturnal flights. A mean estimated 'Stopover After' duration of 1.81 days further indicates that the majority of birds were present for less than two days. This brief pause is not surprising, given that birds have reached a barrier in the form of the English Channel and also given their energetic status (see above). The minimum stopover durations of birds remaining longer than a day were rarely greater than three days (Fig 5) and the standard deviations for estimated 'Stopover After' durations also suggest that few birds had longer durations (Table 1). The mostly likely explanation for birds remaining longer than a day may be that their departure was delayed by unfavourable conditions (eg rain or strong winds).

Nevertheless, some birds remained at the site for longer periods, which, alongside the finding that retrapped birds tended to have lower body mass on first capture relative to

those that were not, suggests that a minority were stopping to refuel. The percentage of refuelling birds is likely to be small, even when allowing for inaccuracies in stopover duration estimation. Indeed, the majority of retrapped birds decreased in mass and only a few birds actually gained any significant amount of mass and therefore fuel (Figs 3 & 4), although the high percentage of decreases may be a consequence of capture effects (Gosler 2001).

The longest recapture histories generally show initial mass loss but an eventual recovery of much of the lost mass (Fig 4). However, given the time expended on these stops, their infrequency in the population and the relatively small fuel gains (typically <1 g; Fig 4), these stopovers appear suboptimal (Hedenström & Ålerstam 1997). Whilst birds are expected to pay a stopover cost – an initial loss in mass while birds locate suitable food sources and/or switch their metabolism from burning to storing fat (Ålerstam & Hedenström 1998) – some of the dramatic initial losses seem more likely to be a consequence of juvenile incompetence in a tiny percentage of the population than typical stopover behaviour.

For birds that increased their fuel stores, FDRs were relatively low, with a mean 'positive' FDR of 2.4% of LBM/day which is similar to those reported for other insectivorous Sylviidae at sites around Europe (eg Bibby & Green 1981; Schaub & Jenni 2000). Refuelling also appears possible in birds making a daytime stop, with evidence for birds 'topping' up their fuel reserves. Indeed, based on six birds that had a mean rate of 0.125 g/hour over a morning, it seems quite possible for birds to gain over one gram in mass during a day.

Migratory strategies

There was no indication that adults and juveniles differed in strategy, except for a subtle difference in fat reserves, and there was no apparent change in strategy with time of year with respect to FDR and fuel reserves. Therefore, both adult and juvenile Grasshopper Warblers clearly accumulate fuel before they arrive on the south coast and it seems plausible that this pre-migratory fuelling occurs either on the breeding grounds or at areas nearby. Grasshopper Warbler breeding habitat may therefore perform two key roles; firstly by providing suitable nesting habitat and sufficient resources for rearing young, and secondly by providing sufficient resources for the completion of the first stage of southward migration.

There was no evidence to suggest that south coast sites such as PVR act as important stopovers (except for the minority of birds that have depleted their reserves on reaching the south coast). Given that only a small percentage of birds stopped at PVR for more than one day and that the fuel stores of those stopping typically decreased, it seems that the south coast is used largely

as a pausing point before crossing the English Channel. However, if mass gains by transient birds that stop for just one day are commonplace (see above), sites that are not used for stopping over but simply ‘topping up’ may still have an important role in the migratory strategy of Grasshopper Warblers.

The level of fuel carried by the average bird passing through PVR theoretically allows for a maximum flight range of 537–747 km. A bird at the higher end of this estimate could therefore reach an area in southwest France between Bordeaux and the Pyrenees. Birds with smaller reserves could still reach this area if like many migrants they utilised tailwinds to increase their range (Åkesson & Hedenström 2000) or ‘topped up’ their reserves during daytime stops. Birds with larger reserves would be able to reach northern Iberia and thus the estimated flight ranges suggest that the southern half of France and potentially northern Iberia are likely to be important refuelling areas for British & Irish Grasshopper Warblers. This prediction is supported by the limited data on the autumn movements of Grasshopper Warblers from Britain & Ireland (Fig 6).

The strategy used by birds once they have refuelled in southwest France is unclear, as there are no autumn recoveries of British or Irish birds between this region and wintering areas in West Africa (Fig 6). Theoretically, birds could accumulate large fuel reserves in this region, enabling them to reach West Africa without refuelling. This strategy would bear similarities to that displayed by the Sedge Warbler in northwest Europe (Bibby & Green 1981), whose pattern of recoveries is strikingly similar to that of the Grasshopper Warbler. However, given the presence of good numbers of Grasshopper Warblers in reedbeds in southern Portugal (Wernham *et al* 2002), it seems likely that this area may also act as a stopover for this species, as is the case for British Reed Warblers (Bibby & Green 1981). Determining habitat use in southwest France and site use between there and West Africa are important ways forward if we are to understand the needs of migrating Grasshopper Warblers more fully.

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