Migratory stopovers of Wrens *Troglodytes troglodytes* on the south-eastern Baltic coast

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Mean body mass, fuel deposition rate and duration of stay were estimated in migrating Wrens in Rybachy on the Courish Spit (Russian Baltic coast). During both spring and autumn migratory seasons, Wrens on average gained mass in Rybachy. Non-transients (i.e. individuals that stopped over for more than one day) gained on average 2.5% of their initial body mass in spring and 2.2% in autumn during their stay. As flight costs in Wrens are likely high, and fuel stores were comparatively low, we argue that these short-distance migrants breeding in the Baltic region and wintering presumably in central Europe and on the British Isles make short migratory flights and probably travel relatively slowly.

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1. Introduction

Although many migrating birds are capable of making spectacular non-stop flights across ecological barriers (e.g. Gill et al. 2005, 2009), most migrants stop over periodically between migratory flights. Migrating birds were estimated to spend on average ca. 85% of the total migration time at stopovers, and spend ca. 65% of energy allocated for migration during stopovers (Wikelski et al. 2003, Chernetsov 2008). The study of migratory stopovers is therefore of great importance for understanding movement ecology of migrating birds. At stopovers migrants find themselves in unfamiliar surroundings (Bairlein 1983, Moore et al. 1990), faced with the need to acquire food rapidly, while balancing conflicting demands between predator avoidance and food acquisition (Cimprich et al. 2005, Lindström 1990, Moore 1994). They have to compete with other migrants and resident birds for limited resources (Moore & Yong 1991, Salewski et al. 2007a), and need to make accurate orientation decisions (Cochran et al. 2004, Muheim et al. 2006). How well migrants offset the costs of migration depends on how well they solve the problems that arise during passage. Solutions of *en route* problems determine the success of a migration. Most important quantitative characteristics of stopovers are their duration and fuel deposition rate

(FDR). These parameters are usually estimated from trapping and retrapping migrants at stopovers in mist-nets (Schaub & Jenni 2000, 2001).

We studied stopover ecology of Wrens *Troglodytes troglodytes* on Cape Rossitten on the Courish Spit (55°09´ N 20°46´ E, south-eastern Baltic coast, Kaliningrad Region of Russia). The aim of this study was to estimate the average stopover duration during spring and autumn migration, FDR and departure fuel stores. We also aimed to identify factors that influence FDR. We tested the hypothesis that migrating Wrens consisted of transients that stopped for one day and resumed their migration during the first night after arrival, and non-transients that made longer stopovers and probably increased their fuel stores. We also compared our FDR and stopover efficiency estimates with the published data on European robins that might have better aerodynamics quality and thus lower energetic flight costs than Wrens.

2. Material and methods

2.1. Data collection

In the eastern Baltic, Wrens are short-distance nocturnal migrants. This is clearly shown by the seasonal pattern of their captures and by the few long-distance recoveries of birds ringed on the Courish Spit (one recovery in Czech Republic, Payevsky 1973; one recovery in southern England, Bolshakov et al. 2001).

In 1994–2006, Wrens were captured in mist-nets in the framework of the trapping project carried out by the Biological Station "Rybachy" in cooperation with Max Planck Research Institute for Ornithology (Radolfzell, Germany). In 1994–2003, the birds were captured in 73 mist nets located in four lines and several isolated nets and small groups. In 2004–2006, the number of mist nets was reduced to 25 located in two net lines. The nets were open from 27 March to 10 June and from 30 June to 1 November. They were open 24 h a day, but birds were only captured during the daytime. Net checks were done every hour from dawn to dusk. For each bird, wing length was recorded to the nearest 0.5 mm as a size proxy, and the birds were weighed to the nearest 0.1 g. Fat score was recorded following Kaiser (1993), and muscle scoring followed Bairlein (1995).

2.2. Data analysis

We used capture-mark-recapture (CMR) models to estimate the probability of stay from the capture-recapture data (Lebreton et al. 1992, Williams et al. 2002). The CMR models estimate daily probabilities of stay that will be addressed as survival rates. These estimates may be viewed as the probability of stay at stopover sites, because it can reasonably be assumed that mortality is insignificant during the rather short stopover duration (Schaub et al. 2001, Schaub & Jenni 2001). The two estimated parameters are the probability that a marked individual that is present at the stopover site at day i is still present at this site at day $i + 1$ (probability of stay,

Φ_i), as well as the probability that a marked individual present at the stopover site at day i is captured at this day (recapture probability, p_i).

The probability that newly caught individuals are transients (individuals whose probability of stay is zero, Pradel et al. 1997) and the probabilities of stay of non-transients can be estimated by fitting a model with an 'age'-dependent structure with the first 'age' class spanning one day (Pradel et al. 1997). The probability that a newly caught individual is a transient is then $\tau = 1 - \Phi_1/\Phi_2$, where Φ_1 is the estimate of the probability of stay of the first and Φ_2 the estimate of the probability of stay of the second 'age' class (Salewski et al. 2007b).

Stopover duration can be calculated from estimates of the probabilities of stay and seniority by simple transformations (Schaub et al. 2001). Seniority is the probability that a marked individual present at the stopover site at day i was present at the site at day $i - 1$ and is used to estimate time that the bird spent at the site before its first capture (Pradel 1996). However, we focus on the probability of stay only, because it has been questioned, whether the seniority probability needs to be included for getting estimates of stopover duration (Efford 2005, Pradel et al. 2005). Stopover length (SL; mean and 95% confidence interval) was calculated as $SL = -1/\ln \Phi$ (Schaub et al. 2001). If a proportion of birds were transients, stopover length of non-transients was calculated as $SL = -1/\ln \Phi_2$. Stopover duration of transients is 1 day per definition.

The models were fitted by MARK 5.1 programme (White & Burnham 1999). We used Akaike's information criterion (AIC) to rank the models (Burnham & Anderson 1998). We evaluated the goodness-of-fit (GOF) of models that did not account for transients by program RELEASE implemented in MARK 5.1.

Fuel loads were calculated as the difference between the measured body mass of each bird and the predicted lean body mass of this individual. Predicted lean body masses were obtained by fitting the regression of body mass on wing length in Wrens with no visible subcutaneous fat deposits (mass = $0.2557 \times$ wing length $- 3.588$; $R^2 = 0.4081$; $p < 0.001$; $n = 202$). Our estimates of fuel load were conservative, as many Wrens with no subcutaneous fat deposits still carried some fat and were not completely lean. It should be also noted that as relatively many Wrens had a muscle score of 3 (Bairlein 1995), protein probably made up a larger proportion in fuel stores of Wrens than in many other small passerine migrants. However, we have no quantitative estimates.

Fuel deposition rate was estimated based on multiple regression model suggested by Schaub & Jenni (2000). This model assumes that birds gain mass during the daytime, this increase being measured in $g \cdot h^{-1}$ (which included both fuel deposition and mass increase due to consumption of food), and lose mass during the night. To accommodate this loss, the second parameter estimated was mass change rate between the days corrected for nocturnal mass loss. It was measured in $g \cdot day^{-1}$ and was the actual fuel deposition rate. FDR was not corrected for body size, i.e. is was measured in actual grams of body mass that could be then transformed into percentages of the initial body mass or of estimated lean body mass.

The models were designed to have zero intercept, model selection was done by backward stepwise elimination. The dependent variable was mass change between

two capture events. The main effects were mass change rate within the day (Δtime, g·h^{-1}) and mass change rate between the days (Δdate, g·day^{-1}). They were always kept in the model, even if non-significant. The additional potential factors (independent variables: wing length, year, progress of season represented as Julian date, JD, and initial body mass) were modelled as interactions with the main effects because of the zero intercept of the model.

3. Results

3.1. Body mass and fuel stores

The mean body mass of Wrens during spring migration (until 10 May) was 9.37 g (SE = 0.020; n = 2083). During autumn passage (after 1 September) it was 9.49 g (SE = 0.012; n = 5027). Both mean body mass (t = 5.18; p < 0.001) and condition index (body mass divided by wing length, t = 4.50, p < 0.001) in autumn were significantly higher than in spring.

The mean fuel load of Wrens at initial capture during spring migration was 4.45% of lean body mass (SE = 0.19; n = 2016), during autumn migration it was 5.29% (SE = 0.11; n = 4982). Predictably, average fuel load during autumn passage was significantly higher than in spring (t = 3.92; p < 0.001).

3.2. Fuel deposition rate

The final model of FDR in spring (Table 1) included wing length (which was positively interacting with both Δtime and Δdate) and initial body mass (which was negatively interacting with Δdate). Furthermore, FDR varied significantly between the years of study as shown by inclusion of many years as significant categorical variables. The final model had an adjusted R^2 = 0.532; $F_{13.597}$=54.4; p<0.0001; SE of estimate = 0.45257. The model predicted a daily body mass increase rate of 0.047 g·day^{-1} (95% CI: 0.039 – 0.055 g·day^{-1}) in an average individual, i.e. a Wren with an average initial body mass and wing length.

In autumn, wing length did not significantly interact with either Δdate or Δtime, initial body mass, like in spring, interacted negatively with Δdate, and progress of the season (increasing Julian date) was positively correlated with Δtime and negatively correlated with Δdate (Table 2). Like in spring, annual variation in FDR was significant. The final model had adjusted R^2 = 0.547; $F_{13.597}$ = 208.6; p<0.0001; SE of estimate = 0.46524. Body mass change rate in an average Wren (a bird with the mean body mass and wing length captured at the median date of autumn passage) was predicted to be 0.030 g·day^{-1} (95% CI: 0.027 – 0.033 g·day^{-1}).

3.3. Stopover duration

The best model that described the variation in daily probability of stay (termed 'survival probability' in the context of this study) assumed a time-since-marking de-

Table 1. The final model for describing fuel deposition rate of Wrens in Rybachy during spring migration. Apart from the main effects, non-significant variables have no entry. Δdate – fuel deposition rate in g·day^{-1}, Δtime – mass change during the day in g·hour^{-1}, MASS∗Δdate – interaction of initial body mass with Δdate, WING∗Δdate and WING∗Δtime – interactions of wing-length (as a proxy for body size) with Δdate and Δtime, respectively.

Effect	Beta	SE	B	SE	t(597)	p-level
Δdate	1.027	0.7955	0.1241	0.0960	1.293	0.1966
Δtime	−1.485	0.7831	−0.1253	0.0661	−1.896	0.0585
MASS∗Δdate	−2.705	0.4030	−0.0340	0.0051	−6.711	0.0000
WING∗Δdate	2.064	0.8895	0.0050	0.0022	2.321	0.0206
WING∗Δtime	2.086	0.7826	0.0036	0.0013	2.666	0.0079
1996	−0.252	0.0287	−0.3904	0.0445	−8.764	0.0000
1998	−0.093	0.0286	−0.1852	0.0567	−3.269	0.0011
1999	−0.088	0.0291	−0.1645	0.0541	−3.039	0.0025
2000	−0.060	0.0286	−0.1353	0.0643	−2.104	0.0358
2001	−0.077	0.0292	−0.1465	0.0556	−2.635	0.0086
2003	−0.072	0.0287	−0.1689	0.0678	−2.491	0.0130
2004	0.065	0.0279	0.4346	0.1859	2.338	0.0197

Table 2. The final model for describing fuel deposition rate of Wrens in Rybachy during autumn migration. Apart from the main effects, non-significant variables have no entry. Δdate – fuel deposition rate in g·day^{-1}, Δtime – mass change during the day in g·hour^{-1}, MASS∗Δdate – interaction of initial body mass with Δdate, JD∗Δdate and JD∗Δtime – interactions of Julian date (progress of season) with Δdate and Δtime, respectively.

Effect	Beta	SE	B	SE	t(3243)	p-level
Δdate	0.934	0.2749	0.0927	0.0273	3.397	0.0007
Δtime	−0.166	0.2931	−0.0177	0.0313	−0.566	0.5712
MASS∗Δdate	−0.284	0.1219	−0.0029	0.0012	−2.332	0.0197
JD∗Δdate	−0.450	0.2200	−0.0002	0.0001	−2.046	0.0408
JD∗Δtime	0.677	0.0799	0.0003	0.0000	8.480	0.0000
1993	−0.047	0.0118	−0.2658	0.0667	−3.982	0.0001
1994	−0.054	0.0121	−0.2096	0.0472	−4.445	0.0000
1995	−0.131	0.0123	−0.3115	0.0294	−10.584	0.0000
1996	−0.194	0.0126	−0.3111	0.0202	−15.427	0.0000
1998	−0.157	0.0127	−0.2965	0.0240	−12.375	0.0000
1999	−0.164	0.0128	−0.3358	0.0261	−12.870	0.0000
2000	−0.045	0.0120	−0.1155	0.0307	−3.762	0.0002
2001	−0.075	0.0122	−0.1741	0.0283	−6.145	0.0000
2002	−0.106	0.0125	−0.1979	0.0233	−8.491	0.0000
2003	−0.073	0.0122	−0.2289	0.0384	−5.955	0.0000
2004	−0.038	0.0119	−0.2863	0.0889	−3.220	0.0013

Table 3. Parameterisation of the best fit model of daily survival rate and recapture probability of Wrens on the Courish Spit in spring. Akaike weight of this model is 0.981.

Daily survival rate	Parameter estimate	SE	Lower CI	Upper CI
Since the second day of stopover, constant throughout the years	0.8181	0.0112	0.7951	0.8390
After the first day of stopover, 1994	0.2006	0.1095	0.0618	0.4888
After the first day of stopover, 1995	No estimate			
After the first day of stopover, 1996	0.3844	0.1145	0.1947	0.6172
After the first day of stopover, 1997	No estimate			
After the first day of stopover, 1998	0.9851	0.1097	0.0971	0.9998
After the first day of stopover, 1999	No estimate			
After the first day of stopover, 2000	No estimate			
After the first day of stopover, 2001	0.8940	0.1286	0.3713	0.9918
After the first day of stopover, 2002	0.0527	0.0519	0.0072	0.2996
After the first day of stopover, 2003	No estimate			
After the first day of stopover, 2004	No estimate			
After the first day of stopover, 2005	No estimate			
Daily recapture probability, constant	0.1876	0.0117	0.1658	0.2115

pendent model, with survival rate from day 1 to day 2 specific in each study year, and 'survival' rate in subsequent days the same across the years of study. Recapture probability in the best model was held constant. For both spring and autumn migration the same model structure showed the best fit (Tables 3 and 4).

Stopover duration of non-transients was 4.98 days (95% CI 4.36 – 4.70) in spring and 6.87 days (95% CI 6.25 – 7.55) in autumn. The proportion of transients (τ) averaged across the years of study was 0.49 in spring and 0.70 in autumn. This means that 49% of Wrens made one-day stopovers (were transients), and 51% stopped over for on average 4.98 days in spring. The respective figures for autumn passage were 70% of transients and 30% of birds stopping for on average 6.87 days.

An average non-transient Wren gained 0.047 g·day^{-1} × 4.98 days = 0.234 g (2.5% of initial body mass) in spring and 0.030 g·day^{-1} × 6.87 days = 0.206 g of fuel, or 2.2% of initial body mass, in autumn.

4. Discussion

In both seasons, initial body mass had a significant negative effect on FDR, with heavier birds gaining mass more slowly (Tables 1, 2). This effect is often found in the studies of fuel deposition rate based on captures and recaptures (Loria &

Table 4. Parameterisation of the best fit model of daily survival rate and recapture probability of Wrens on the Courish Spit in autumn. Akaike weight of this model is 0.939.

Daily survival rate	Parameter estimate	SE	Lower CI	Upper CI
Since the second day of stopover, constant throughout the years	0.8645	0.0060	0.8522	0.8759
After the first day of stopover, 1994	0.4298	0.1013	0.2511	0.6289
After the first day of stopover, 1995	0.7841	0.1125	0.4969	0.9303
After the first day of stopover, 1996	No estimate			
After the first day of stopover, 1997	No estimate			
After the first day of stopover, 1998	No estimate			
After the first day of stopover, 1999	No estimate			
After the first day of stopover, 2000	No estimate			
After the first day of stopover, 2001	0.0664	0.0461	0.0163	0.2341
After the first day of stopover, 2002	No estimate			
After the first day of stopover, 2003	0.0702	0.0487	0.0172	0.2460
After the first day of stopover, 2004	No estimate			
After the first day of stopover, 2005	0.0538	0.0530	0.0073	0.3047
Daily recapture probability, constant	0.1409	0.0058	0.1298	0.1527

Moore 1990, Fransson 1998, Schaub & Jenni 2000, Chernetsov 1998). It may be a natural phenomenon, but might also be an artefact if the birds losing weight have higher mobility (and thus higher probability of capture) compared with those gaining weight. It is worth noting that in spring, wing-length had a positive effect on fuel deposition rate. It might indicate that males who have on average longer wings, gained mass more rapidly, probably because of greater pressure to travel fast and to arrive early (Kokko 1999). It is worth noting that in autumn, wing length was not a significant effect. It strongly suggests that higher FDR in larger birds was not just an allometric effect, as it should have occurred in both seasons equally. In both seasons, annual variation of fuel deposition rate (and of proportion of transients) was significant.

Our analysis suggests that a substantial proportion of migrating Wrens actually stop over in Rybachy on the Courish Spit and that they generally gain mass on Cape Rossitten in both seasons. Approximately one-half of birds in spring and 70% in autumn do not stop for more than one day, i.e. they resume migration on the next night after arrival. The remaining birds stop for 5–7 days. However, the rate of their mass gain is rather small, they increase their fuel stores by just 2.2–2.5% during the stopover.

Wrens have relatively short and rounded wings, which may resultin poorer aerodynamic quality than in most other passerine nocturnal migrants (Pennycuick

1989, Videler 2005). Due to this, their flight costs may be higher than in other passerines with similar body mass that have longer and more pointed wings (e.g. Willow Warblers *Phylloscopus trochilus*, Chiffchaffs *Ph. collybita*).

Fuel loads of Wrens in our study can be compared with the mean fuel load of European robins *Erithacus rubecula* estimated by Tsvey (2008) at the same site by the same method which was 6.0% for both seasons pooled (SD = 7.2; n = 91608). This value was significantly higher than our estimate for the Wren in either season (t-test, both p<0.001).

Fuel deposition rate of Wrens was 0.047 g·day^{-1}, i.e. 0.52% of lean body mass in spring, and 0.30 g·day^{-1}, i.e. 0.33% in autumn. European robins have a very low FDR in spring (0.05% of lean body mass per day, i.e. very close to 0), but their autumn FDR, 0.44% of lean body mass per day, was even slightly higher than in Wrens (Tsvey 2008). The mean duration of stay of European robins that stop over for more than one day on the Courish Spit is 4.87 days in spring and 5.78 in autumn (calculated from Fig. 25 in Tsvey 2008), the total fuel store increase in this species is 0.24% in spring and 2.54% in autumn.

Given relatively low fuel loads of Wrens that make stopovers on the Courish Spit and their low fuel deposition rates, we assume that during both spring and autumn migration, Wrens make relatively short flights that probably do not last during the whole night. It is not improbable that their low fuel loads are a consequence of their presumed low aerodynamic quality and relatively high flight power. With their short wings, Wrens may suffer greater costs of carrying extra fuel than many other passerine migrants (Chernetsov 2010). Wrens are short-distance migrants in our area, probably breeding in the Baltic region and wintering in central and western Europe and on the British Isles (Payevsky 1973, Bolshakov et al. 2001). They are known to regularly occur in winter as far north as Leningrad Region (Malchevsky & Pukinsky 1983), so in autumn, Wrens may be not pressed to move towards the south very rapidly. Due to their relatively high flight costs, Wrens may be energy-minimising migrants in the sense of the current optimal migration theory (Weber & Houston 1997, Hedenström 2008).

Acknowledgements

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