



УДК 591.524.23

INFLUENCE OF FUEL LOAD AND WEATHER ON TIMING OF COMPLETING NOCTURNAL FLIGHTS IN REED WARBLERS, *ACROCEPHALUS SCIRPACEUS*, DURING SEASON MIGRATIONS

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ABSTRACT

Time of completing nocturnal migratory flights in passerines is essential for their safety during landing and stopover site selection. I studied landing time, fuel stores and weather at landing in Reed warblers migrating through the Courish Spit on the Baltic Sea in autumn and spring. I used data on 697 Reed warblers tape-lured into a habitat atypical of this species in 1999–2002. In both seasons, more than one-half of all birds (59% in autumn, 56% in spring) were captured in the last two hours before sunrise, while the rest in the beginning and middle of the night. I tested the hypothesis that early landing could be caused by take-offs in the beginning of the night with small fuel stores, not sufficient for the flight throughout the night. It was confirmed only for the young birds that migrated in the second half of the autumn season. Comparing wind assistance, cloud cover and precipitation in the days of landings in the beginning-middle of the night versus late night, I found no impact of these potentially important weather parameters on the temporal distribution of early and late landings. It is assumed that early landings of some Reed warblers could be caused by short-term nocturnal flights not directly related to the migration rush to the target.

Key words: *Acrocephalus scirpaceus*, nocturnal landing, Reed warbler, spring and autumn migration, weather and stopover factors

ВЛИЯНИЕ ЭНЕРГЕТИЧЕСКОГО СОСТОЯНИЯ И ПОГОДЫ НА ВРЕМЯ ЗАВЕРШЕНИЯ НОЧНЫХ ПОЛЕТОВ У ТРОСТНИКОВЫХ КАМЫШЕВОК, *ACROCEPHALUS SCIRPACEUS*, ВО ВРЕМЯ СЕЗОННЫХ МИГРАЦИЙ

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РЕЗЮМЕ

Время завершения ночных миграционных полетов у воробьиных имеет важное значение для их безопасности во время посадки и выбора места остановки. Я исследовал погоду, время приземления и энергетическое состояние тростниковых камышевок во время их окончания ночного полета в периоды осенней и весенней миграции на Куршской косе в Балтийском море. Я использовал данные по 697 тростниковым камышевкам, пойманым при воспроизведении их песен в не типичном для них биотопе в 1999–2002 гг. В оба сезона более половины всех птиц (59% осенью, 56% весной) были пойманы в последние два часа перед восходом солнца, в то время как остальные птицы были пойманы в начале и в середине ночи. Я проверил гипотезу о том, что раннее приземление могло быть причиной старта птиц в начале ночи с небольшими энергетическими ресур-

сами, не достаточными для полета в течение всей ночи. Это предположение нашло подтверждение только для молодых птиц, которые мигрировали во второй половине осеннего сезона. Сравнивая направление ветра, облачность и наличие дождя в дни с приземлением птиц в начале-середине ночи, с одной стороны, и в конце ночи, с другой стороны, я не нашел значимого влияния этих потенциально важных метеорологических параметров на временное распределение ранних и поздних приземлений. Предполагается, что ранние приземления некоторых тростниковых камышевок могли быть вызваны непродолжительными ночными полетами, которые прямо не были связаны с миграционными бросками птиц к их цели.

Ключевые слова: *Acrocephalus scirpaceus*, ночное приземление, тростниковая камышевка, весенняя и осенняя миграция, погодные и остановочные факторы

INTRODUCTION

Knowledge about departure and landing in nocturnal passerine migrants is very important to understand their migration strategies. Time of departure, the amount of fuel stores and the weather during departure and subsequent flight in many respects determine the duration of their flights. The time of flight termination may determine not only its distance, but also successful stopover site selection. The original idea of when passerines begin and end their migratory flights were obtained mainly from the moon-watching (Lowery 1951) and radar studies (see the review of Kerlinger and Moore 1989). The mass appearance of flying passerines in the early night was explained by their synchronous departures shortly after sunset. The reduction of numbers aloft around midnight was interpreted as the end of a night flight by many migrants (Kerlinger and Moore 1989). Observations of migrants in the searchlight beam (ceiometer), radio tracking data and the method of retrapping of ringed birds in high nets shed light on the take-off time (in particular, they showed a very large variation in departure time in some species of passerines) and many features of departure behaviour (Bulyuk and Tsvey 2006; Bolshakov et al. 2007; Schmaljohann et al. 2011). Unfortunately, this is not true of our knowledge when individual birds complete nocturnal flights, what factors influence their decision to land, and how they choose landing locations.

Even though some nocturnal passerines can land at different hours of the night, there is evidence that many migrants prefer to land at dawn (Bolshakov 1981; Bruderer and Liechti 1995; Bolshakov et al. 2003a, b). Factors responsible for the decision of the birds to stop flying in the early hours of the night remain unclear. Theoretically, early landings of individual birds may be due to several reasons. 1. Small

departure fuel stores, insufficient for long flights (*the energetic hypothesis*). This hypothesis predicts that the departure fuel stores of early landed birds will be on average lower than in birds that complete flights in the end of the night. 2. Unfavourable weather conditions encountered en route (*the weather hypothesis*). These adverse weather conditions include, first of all, opposite or opposite side wind which makes migration either impossible (in strong winds) or energetically unfavourable (at moderate winds; Liechti 2006). Overcast and/or rain can reduce visibility and make plumage wet, thus impairing the ability to orient visually, and increasing flight costs. In these circumstances, many birds will probably try to interrupt flight (Richardson 1978, 1990). If this is correct it should be expected that in the nights with early landings of birds wind and cloud conditions will be poorer, respectively, for migration flight and orientation than during the later landings of migrants. Early landings are more likely in the nights with rainfall in the beginning or middle of the night than in the nights without precipitation.

The energetic and weather hypotheses are not mutually exclusive, as landing time may depend on both condition and weather factors. Migrants with large fuel stores and thus a high motivation to continue migration might be less responsive to weather condition than birds with low fuel stores. Therefore birds landing early and late into the night may differ not only by their fuel load but also by weather conditions in landing nights.

In this paper I studied landing time and fuel stores and weather at landing in a long-distance nocturnal migrant, the Reed warblers *Acrocephalus scirpaceus*, migrating through the Courish Spit on the Baltic Sea in autumn and spring. My aims were (1) to obtain the data on exact landing time of individual birds; their energetic condition at landing; weather variables at

the landing night; and (2) to test the energetic and weather hypotheses explaining variation in landing time in nocturnal migrants.

In this work I used data on Reed warblers captured during landing in a habitat atypical of this species into which they were tape-lured. It is assumed that the migrant songbirds use acoustic information as distant cues for habitat selection when ceasing flight (Herremans 1990; Schaub et al. 1999; Mukhin et al. 2005a, 2008). Apart from radio tracking of migratory passerines until their landing (Cochran et al. 1967; Cochran and Wikelski 2005) and trapping of birds in the high nets during landing (Bolshakov et al. 2003a, b; Bulyuk 2006, 2012; Bulyuk and Tsvey 2006, 2013), this method is one of the few ways to study the time of landing, body condition of migrants and weather conditions during landing. At my trapping site the number of Reed warblers captured without tape-luring is very low (see Discussion). The obvious reason for this is that mist-netting was performed in willow scrub and not in a reedbed, i.e. in the habitat atypical of the Reed warbler. Therefore, we can safely assume that Reed warblers in our tape-luring sample were not attracted from some nearby areas, but from aloft. One could argue that tape-luring attracts birds not otherwise prepared to land. However, I assume that this is not the case: tape-luring triggers landing in migrants that are motivated to terminate their flight anyway. Without tape-luring these birds would have flown some 10–15 km further and would have landed in a reedbed on the coast of the Courish Lagoon, but I think it unlikely that they would have flown 150–200 km more. It certainly remains an assumption, albeit, in my opinion, a likely one.

MATERIAL AND METHODS

Study site and method

Data on the temporal distribution of landing Reed warblers, their age and body condition, and weather during the landing were collected at a specially designed field site on the Courish Spit (55°05'N, 20°44'E; see Fig. 1 in Mukhin et al. 2008). Between 1999 and 2002, I with colleagues used the song tape-lure method to capture Reed warblers landing in a habitat atypical of this species in the transition gap between pine plantations and high sand dunes partly covered by willow scrub. The nearest reed stands were located 4 km to the southwest and 10 km to the

northeast of the study site. In certain years captures were carried on during most of the nights during the following periods: 1999: 22 July – 11 September; 2000: 30 April – 17 October; 2001: 30 April – 23 September; 2002: 27 July – 11 September. Birds were trapped in standard mist-nets (height 7×2 m, 14-mm mesh) erected in one (1999) or two (2000, 2001) squares or in a line (2002) extending 81–110 m, depending on the year. High nets (Bolshakov et al. 2000) were also erected between the two squares of the standard mist-nets (2000–2002) (see Fig. 1 in Mukhin et al. 2008). All nets were opened at sunset and closed 30–40 min after sunrise (1999) or 20 min before sunrise (2000–2002). The acoustic system was centred in a square or in the middle of a net line and included 2 car tape players with 30 W loudspeakers (frequency range 50–20,000 Hz) directed toward the northeast and southwest. In 1999, both Reed warbler and Marsh warbler *Acrocephalus palustris* songs were played continuously (45-min repeat sessions of each species) between sunset and sunrise. In 2000 and 2002, only Reed warbler songs were played; in 2001, again both Reed warbler and Sedge warbler *A. schoenobaenus* songs were played. Studies of Mukhin et al. (2005a, 2008) have shown that Reed warblers equally responded to tape-lure playing as the conspecific song, and the Marsh and Sedge warbler songs. Under optimal conditions at this site, human hearing distance was assessed to be approximately 1,000 m at ground level. The nets were checked each hour with a torch during the whole night. Trapped birds were weighed immediately after capture to the nearest 0.1 g, in the morning, other biometrical information was collected following the guidelines of ESF programme (Bairlein 1995). All birds captured at night were released within 1 h after dawn at 250 m from the capture site.

In this paper, I used data on 697 Reed warblers captured during seasonal migrations in spring from 4/5 May until 13/14 June (262 individuals); in autumn from 20/21 July until 26/27 September (435 individuals: 223 adults and 212 juveniles). A relatively small proportion of young individuals in autumn is due to the fact that the analysis included only fully moulted birds of this age group, as many young birds that are actively moulting, even in its last phase, can make nocturnal flights are not associated with autumn migration (Bulyuk et al. 2000, 2009; Mukhin 2004).

To test the energetic hypothesis, I calculated arrival fuel load (AFL) at landing, and the departure

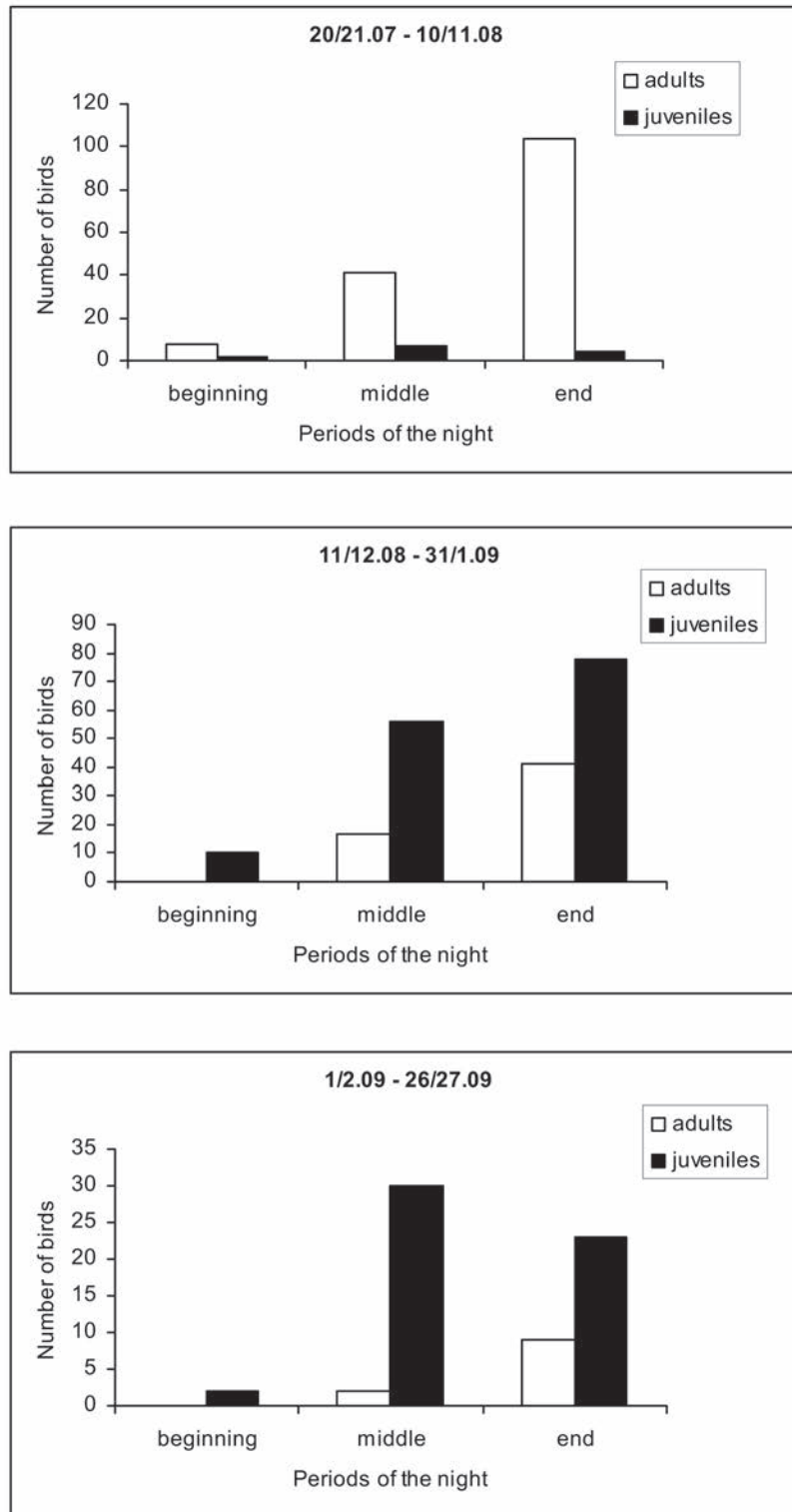


Fig. 1. Numbers of adult and juvenile Reed warblers captured at the study site during landing at the beginning, middle and end of the night in different autumn periods, 1999–2002.

fuel arrival (DFL) of the same individuals. AFL is the amount of fuel at arrival relative to lean body mass (LBM):

$$\text{AFL} = (\text{BM}_{\text{arrival}} - \text{LBM}) \cdot \text{LBM}^{-1},$$

where $\text{BM}_{\text{arrival}}$ is the body mass at arrival.

I calculated the mean mass of lean Reed warblers (fat score 0) with a given wing length for birds trapped in the first two morning hours in Rybachy (12 km north of the study site) in standard mist nets during migratory stopovers in 1994–2010 by linear regression (adults: mass = 1.465 + 0.147·wing; $R^2 = 0.152$; $n=345$; $P<0.0001$; juveniles with completed moult: mass = 1.487 + 0.141·wing; $R^2 = 0.097$; $n=80$; $P<0.001$).

$$\text{DFL} = \text{AFL} + \Delta t \cdot \text{HFLL}$$

where Δt is the number of hours in nocturnal flight between departure and landing, and HFLL is hourly fuel load loss.

Reed warblers are known to take off for nocturnal migratory flights during the first three hours after sunset (Åkesson et al. 2001; Bolshakov et al. 2003a; Bulyuk 2010, unpublished data). To calculate the DFL, I assumed that all Reed warblers that landed in the middle and in the end of the night had taken off on average in the second hour after sunset. Therefore, the duration of their nocturnal flights (Δt) was estimated as the difference between the landing hour and the second hour after sunset. Field and experimental estimates of power requirement for migratory flight yield very low cost of flight in nocturnally migrating passerines (Klaassen 2000; Wikelski et al. 2003). In small migrating passerines similar in size to the Eurasian Reed warbler mass loss during nocturnal migratory flight, obtained by Nisbet et al. (1963) and Hessel and Lambert (1980), was on average 0.9% of body mass per hour. I assumed that the loss of body weight was mainly due to fuel load and used this value as HFLL.

To test the *weather hypothesis*, I studied the relationship between landing time and weather variables that could have a strong influence on the decision to land by passerine migrants: wind, cloud cover, precipitation.

Wind condition at the night of landfall was estimated by the tail wind component (TWC, $\text{m}\cdot\text{s}^{-1}$): $V_w \cdot \cos(\phi_t - \phi_w)$, where V_w is wind velocity, ϕ_t is the mean migration direction in Reed warblers and ϕ_w is wind direction. Recoveries of Reed warblers ringed

on the Courish Spit during passage and reported from the migratory route suggest a mean direction of 51° for spring migration and 232° for autumn migration (Bolshakov et al. 2001). I used both surface and high altitude TWC in the analysis. Surface TWC was calculated from hourly measurements of the wind at the study site. The velocity of the surface wind was estimated using the Beaufort scale, and its direction was classified into 16 categories. Surface TWC at the hour of landing was used in the analysis. All wind data at c. 150 and at c. 750 m a.g.l. were taken from wind balloon data at 0300 hours EEST in Kaliningrad and Łeba (50 and 185 km S and SW of the study site, respectively), obtained through British Atmospheric Data Centre (<http://badc.nerc.ac.uk>).

Cloud cover was recorded hourly from the sunset to sunrise in the study site on a 0–10 scale, where 0 is clear and 10 is overcast.

Rain (the presence or absence) was recorded hourly from the sunset to sunrise at the study site.

Data analysis

To test the energetic and weather hypothesis, I divided Reed warblers into those that were captured during landing in the beginning of the night (first three hours after sunset), middle of the night (more than three hours into the night but two hours before sunrise) and in the end of the night (in the last two hours before sunrise).

To study significance of variation in DFL in these groups, as well as the difference in TWC variables during their landing, I used general linear models (GLM). DFL and TWC parameters were dependent variables. The time of landing was a fixed factor. In spring landing in the beginning, middle and end of the night was coded as 1, 2 and 3, respectively. In autumn few birds were captured in the beginning of the night, which forced me to pool them with the birds caught in the middle of the night. Therefore, in this season the time of the landing was a two-level factor. Another fixed factor was the progress of the season. It was a two-level factor in both seasons. In spring it was scored by date of 20 May, and in autumn by date of 15 August. When testing both hypotheses I used a full factorial multivariate GLM analysis. Pairwise comparisons of means for each significant effect were performed by Scheffe test using the Least Squares Means statement of the GLM procedure.

To test whether cloud cover and rain caused earlier landing, I compared proportions of captures in the beginning-middle of the night vs. the end of the night by contingency tables, (1) when overcast was recorded throughout the night vs nights when the sky was clear or partly cloudy (≤ 5 points), (2) in the night with overcast but without rain vs nights with rain in the beginning or middle of the night.

To determine the combinations of DFL and weather factors (TWC at various heights, cloud cover and the presence of rain at the hour of catching birds), and to test for their possible impact on the probability of landing in the beginning-middle and in the end of the night, I also used a binary logistic regression. Landing in the beginning-middle of the night vs. in the end of the night (coded as 1 and 2, respectively) was the dependent variable. DFL, surface TWC, high altitude TWC at c. 150 and at c. 750 m, cloud cover and rain at the hour of landing birds were independent variables. Another independent variable was the size of moon disk (proportion of the full moon) when it was $> 1^\circ$ above the ground level (1) in the beginning and (2) in the middle of the night. This was done to see how the increased visibility with growing moon disk influenced the likelihood of landing in the beginning-middle and in the end of the night, and whether the “lunar” factor was linked to other explanatory variables. Model selection was done by forward stepwise inclusion. I also ran backward selection procedures to examine the consistency of variable selection.

In autumn among young Reed warblers, unlike adult birds, not all individuals could be migrating (see Discussion). To focus attention on the possible age differences in the behaviour of birds in this season, all the statistical procedures for adults and young birds were carried out separately. All means are reported \pm SD. Statistical analyses were performed in the statistical package SPSS for Windows (version 16.0).

RESULTS

Seasonal features of landing

In both seasons some flying Reed warblers started to terminate their flights and to be trapped in the mist nets in the end of the first hour after sunset. The number of these birds, however, was small (5 individuals in autumn and 4 in spring). In general, 5.1% of Reed warblers were captured in the beginning of

the night (first–third hour after sunset) in autumn. In this season, most birds (59.5%) were trapped during the landing in the end of the night (in the last two hours before the sunrise). More than one-third of the birds (35.4%) were caught in autumn in the middle of the night (i.e. between the third hour after the sunset and two hours before the sunrise; Fig. 1). As shown in Fig. 1, in autumn age ratio birds terminating flight varied with the progress of the season, and with the progress of the night. Among adult Reed warblers the proportion of individuals caught in the end of the night was significantly greater than in juveniles (69.4% and 49.5% respectively; Chi-square test: $\chi^2_1=17.74$, $p=0.0001$). This trend was noted throughout the autumn season. In spring, like in autumn, more than one-half of Reed warblers (55.7%) were captured landing in the last two hours before sunrise. In the former season, however, the proportion captures in the beginning of the night (13.4%) was significantly greater than in autumn (Chi-square test: $\chi^2_1=15.01$, $p=0.0001$). The proportion of such birds increased noticeably from the beginning to the end of the spring migratory season (Fig. 2).

Testing the energetic hypothesis

During autumn migration, the estimated departure fuel load (DFL) of juvenile Reed warblers was on average higher than in adults (0.275 ± 0.115 , $n=212$ and 0.210 ± 0.099 , $n=223$ respectively; T-test: $t=6.32$, $df=433$, $p<0.0001$). Spring DFL of landing Reed warblers (0.083 ± 0.059 , $n=262$) was on average smaller than in autumn in both age groups (adults, T-test: $t=17.31$, $df=483$, $p<0.0001$; juveniles, T-test: $t=23.37$, $df=472$, $p<0.0001$).

GLM analysis of variation in DFL in Reed warblers that landed during spring migration showed no significant differences for “Landing time” and “Season progress” predictor variables and their interaction ($F_{5,256}=1.91$, $p=0.093$). GLM analysis of variation in DFL of adult Reed warblers in autumn showed significant difference only for the “Season progress” ($F_{1,219}=11.43$, $p=0.001$). Adults captured when landing in the first half of the autumn season had lower DFL than those captured in the second half of the season (0.197 ± 0.097 , $n=173$ and 0.256 ± 0.096 , $n=50$, respectively). In juvenile Reed warblers in autumn significant difference in DFL was only recorded for the “Landing time*Season progress” interaction ($F_{1,208}=7.88$, $p=0.005$). If in the first half of the season

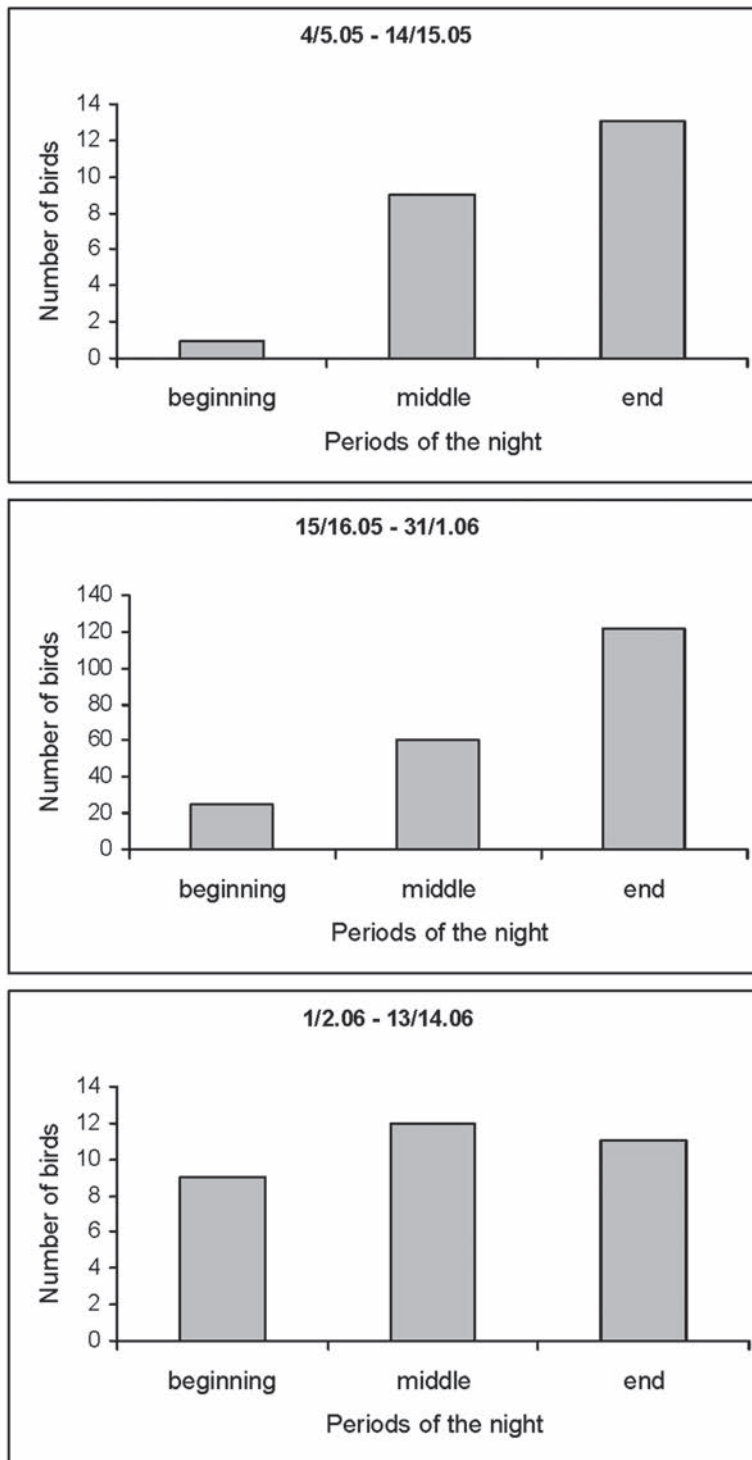


Fig. 2. Numbers of Reed warblers captured at the study site during landing at the beginning, middle and end of the night in different spring periods, 2000–2001.

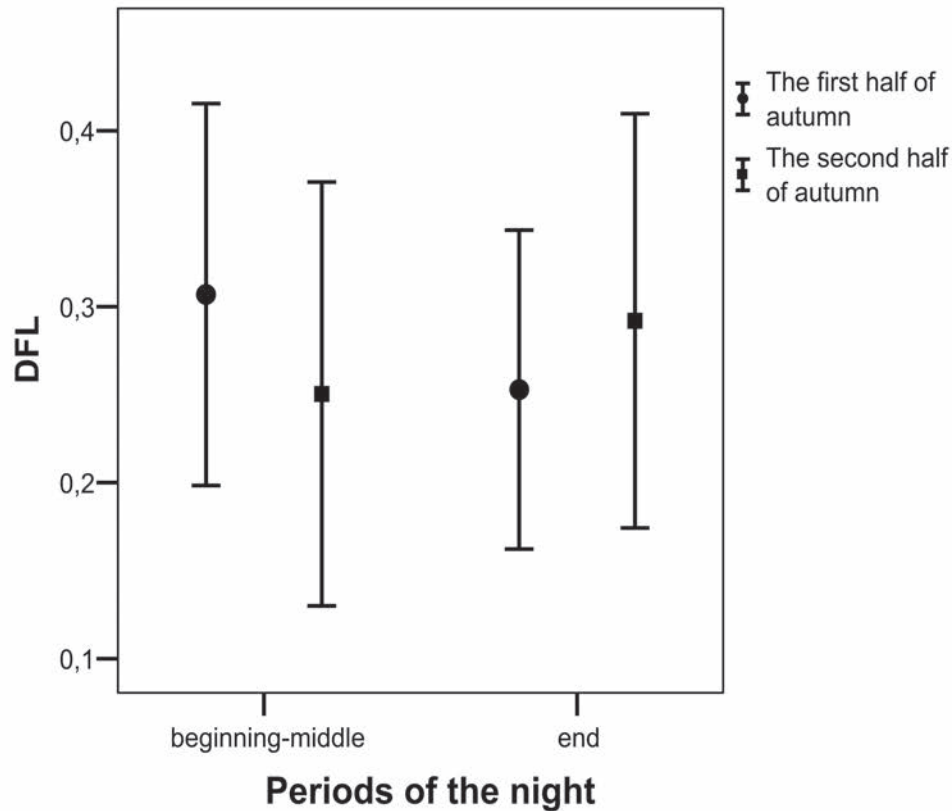


Fig. 3. Departure fuel load (DFL) of juvenile Reed warblers captured at the study site during landing at the beginning-middle and the end of the night in the first and the second half of autumn season. Means \pm SD are shown.

DFL in young Reed warblers landing in the beginning and middle of the night was on average higher than in the end of the night ($P=0.036$). In the second half of the season, conversely, DFL in young Reed warblers landing in the beginning and middle of the night was lower than in the end of the night ($P=0.037$; Fig. 3).

Testing the weather hypothesis

In spring Reed warblers migrated in more favourable wind conditions than in autumn (Table 1). In spring, average TWC at 150–750 m a.g.l. in the nights when the Reed warblers were caught during landing was significantly higher than in the nights when no birds were observed (4.3 ± 4.4 m/s, $n=76$ and 0.9 ± 6.8 m/s, $n=58$ respectively; T-test: $t=3.48$, $df=132$, $p=0.001$). A similar pattern of significant difference in high-altitude TWC between nights with vs. without landings was noted in autumn for both adult and first-year Reed warblers (adults: -0.3 ± 5.2 m/s,

$n=152$ and -2.8 ± 5.6 m/s, $n=168$ respectively; T-test: $t=4.11$, $df=318$, $p=0.0001$; juveniles: -0.6 ± 4.9 m/s, $n=170$ and -2.7 ± 6.0 m/s, $n=150$ respectively; T-test: $t=3.53$, $df=132$, $p=0.0001$).

In both seasons TWC at the same altitude in the nights with recorded landings of Reed warblers differed little between the parts of the night (Table 1). A GLM analysis of variation in TWC for “*Landing time*” and “*Season progress*” predictor variables and their interaction showed significant differences only for “*Season progress*” (1) in spring, and (2) in autumn in juveniles. In both cases, TWC at 150 m and 750 m a.g.l. was significantly worse for migration in the first half of the season than in its second half.

Comparing the number of Reed warblers landed in the beginning and middle of the night vs. the end of the night with overcast on the one hand and clear skies or low cloud cover, on the other, showed no significant difference between them during either spring or autumn migration of adults and juveniles.

A similarly negative result for both seasons was observed when the number of birds that landed in the beginning and middle of the night vs. the end of the night with overcast without rain and with rain at the beginning-middle of the night.

Forward stepwise inclusion in the logistic regression analysis DFL, all weather parameters and the size of the moon disk for the spring data yielded no reliable model. For the autumn data a reliable model was obtained for juveniles only, and with only one predictor, size of moon disk in the middle of the night ($\chi^2_1=12.89$, $p=0.0001$). This model predicts that the probability of catching landing Reed warblers in the beginning and middle of the night was higher when the visible part of the moon disk was larger. This prediction had a very small power (Nagelkerke rho-squared: 0.088).

DISCUSSION

Even though Reed warblers showed rather large variation in departure time, most individuals take off in the second and third hour after the sunset (Åkesson et al. 2001; Bolshakov et al. 2003a; Bulyuk 2010). Very little is known about when Reed warblers complete their nocturnal migratory flights and what factors influence the time of their landing. Analysis of nocturnal captures of landing Reed warblers caught in spring into nets elevated above the canopy at a site where this species makes stopovers and breeds, showed that birds completed nocturnal flights since the middle of the night with a peak in the last two hours before sunrise (Bolshakov et al. 2003a; Bulyuk 2006).

To study the time of landing in Reed warblers, I used data on captures during landing in a habitat atypical of this species. Reed warblers chose this place to stop responding to the playback of their species-specific song. It is assumed that Reed warblers use acoustic information as distant cues for habitat selection when ceasing flight (Herremans 1990; Schaub et al. 1999; Mukhin et al., 2005a, 2008). The fact that none of the Reed warblers caught and released at the point of observation was caught during the departure in the next nights indirectly indicates that the song itself does not attract birds, if they have no motivation to land. Therefore, the “methodological factor” could not significantly affect the time schedule of landings of Reed warblers.

The results of this study showed that more than one-half of migrants completed nocturnal flights in the end of the night. However, many birds were captured when landing in the middle of the night, and a small number even in the beginning of the night soon after departure (Figs. 1, 2). Why did not all birds migrate until the end of the night? What factors were responsible for the early landings? I proposed two hypotheses to explain the landings in Reed warblers in the beginning and middle of the night.

One explanation is that flight duration is controlled by their fuel stores (*the energetic hypothesis*). Birds that departed from a stopover in the beginning of the night with small fuel stores could not fly during the whole night. Comparing the estimated DFL of Reed warblers caught the landing in different periods of the night, I found confirmation of the predictions of this hypothesis only for the young birds that migrated in late autumn (Fig. 3).

Short nocturnal flights in Reed warblers and thus early landings could be due to unfavourable weather conditions during their flight (*the weather hypothesis*). However, comparing TWC, cloud cover and precipitation in the dates of landings in the beginning-middle of the night and at the end of the night, I did not find that these weather factors important for flight costs and orientation significantly influenced the temporal distribution of landings. The lack of confirmation for the energetic (with the exception of young birds in late autumn) and weather hypotheses raises a quite natural question: why some birds ceased flight in the beginning or middle of the night?

Probably some early landings could be due to other causes. In both seasons these brief night flight could be habitat-related. The Reed warbler is a habitat specialist. During both breeding season and migrations these birds prefer reedbeds, thriving along the outskirts and growing in water. However, not all Reed warblers during migration after a night flight stop in similar habitats. In field station Fringilla located 150 m away from the place of the present investigation on the border of a pine forest with shrubs of willow a total of 175 Reed warblers have been captured in stationary funnel traps (for a description of the traps, see Payevsky 2000) over a 45-year period (Mukhin et al. 2005a). Completing nocturnal flights at such suboptimal site, migrants can make short flights during the next night looking for a more favourable place refuel (cf. Ktitorov et al. 2010; Smolinsky et al. 2013).

Table 1. Mean TWC (\pm SD) in the dates of landing of Reed warblers at different periods of the night.

Season	Altitude	Period of the night		
		beginning of the night	middle of the night	end of the night
Spring	surface level	0.6 \pm 1.0 m/s, n=35	0.9 \pm 0.9 m/s, n=81	0.8 \pm 1.0 m/s, n=146
	at c. 150 m	3.9 \pm 3.0 m/s, n=35	4.6 \pm 3.3 m/s, n=81	4.3 \pm 3.2 m/s, n=146
	at c. 750 m	4.8 \pm 3.3 m/s, n=35	5.4 \pm 3.9 m/s, n=81	5.3 \pm 3.9 m/s, n=146
Autumn; adults	surface level	1.4 \pm 1.8 m/s, n=8	0.6 \pm 1.3 m/s, n=61	0.8 \pm 1.8 m/s, n=154
	at c. 150 m	-1.0 \pm 5.1 m/s, n=8	-0.3 \pm 3.7 m/s, n=61	0.1 \pm 4.3 m/s, n=154
	at c. 750 m	-1.5 \pm 4.4 m/s, n=8	-0.9 \pm 4.7 m/s, n=61	-0.5 \pm 4.9 m/s, n=154
Autumn; juveniles	surface level	0.7 \pm 1.6 m/s, n=14	1.3 \pm 2.2 m/s, n=93	1.0 \pm 2.3 m/s, n=105
	at c. 150 m	-0.1 \pm 4.2 m/s, n=14	-0.5 \pm 4.8 m/s, n=93	-0.8 \pm 4.7 m/s, n=105
	at c. 750 m	-1.4 \pm 5.0 m/s, n=14	-0.7 \pm 5.5 m/s, n=93	-0.8 \pm 5.2 m/s, n=105

In spring the birds that were completing migration and were close to the goal could make short nocturnal flights to find the location of nesting. Not surprisingly, the number of such birds increased significantly from the beginning to the end of the spring season (Fig. 2), and they first responded to the sound trap in the beginning-middle of the night. These birds could make short nocturnal flights to find the location of nesting. The presence of such short movements in nocturnal passerine migrants may be indicated by the data on capture birds in the middle of the night in high mist nets at the site where they had been ringed one year earlier (Bulyuk 2006), as well as by the data on the two Reed warblers, caught in the Courish Spit at the possible end of the spring migration. One of them (ring VC 5042) was caught for the first time on the eastern shore of the Courish Lagoon in Lithuania in Ventes Ragas 26.05.1996, and a day later – on the Courish Spit in Rybachy, 32 km south-west of the first place (Bolshakov et al. 2002). Another bird (XG 76 720) was caught in Rybachy 22.05.2010 and 10.06.2010 in Ventes Ragas (Bolshakov et al. 2011). Considerable space of lagoon waters between the two points catch is a good reason to assume that the birds have overcome them during a night flight.

For some juveniles in autumn early landings could result from brief movements related to the search for the future breeding place and/or recognition of the territory (creation of the navigation map), where they will strive to arrive to in spring (Bulyuk et al. 2000, 2009; Mukhin 2004; Mukhin et al. 2005b). Since these non-migratory night flights juveniles perform in sufficiently early age, still in moult, to exclude them from the analysis I used data only for the juveniles with completed moult of body-feathers (see

Methods). However, some juveniles may make such movements also after moult. It might explain slight but significant increase in the probability of catching landing Reed warblers at the beginning-middle of the night with increasing size of moon disk in the middle of the night. Size of moon disk was a factor that contributed strongly enough to the probability that juveniles in active moult performed non-migratory movements over long distances (Bulyuk et al. 2009). I cannot rule out that high proportion of these birds in the first half of the autumn season was the cause of high DFL in young birds landed in the beginning-middle of the night (Fig. 3).

Comparing wind conditions in the nights when Reed warblers were captured during landing, and in the nights when they were not recorded, I found that in the former case the conditions for nocturnal flight were much more favourable than in the latter case. Weather conditions are known to be an important factor contribution to the decision to take off (Alerstam 1990; Berthold 2001; Newton 2008). Reed warblers can choose weather to carry out nocturnal migratory flights on the basis of changes in atmospheric pressure (Åkesson et al. 2002). It cannot be ruled out, however, that they can make mistakes when assessing wind conditions. In such cases, some birds will probably stop flying soon. We may have captured them in the beginning of the night. It is noteworthy that high-altitude wind (c. 750 m a.g.l.) in the dates of landings in the beginning of the night was always less favourable for migration than in the dates with landings in the middle and end of the night (Table 1). As among birds grounded in the beginning of the night many may have been making habitat-related flights (see above), and because I only used wind

balloon data during the second half of the night (see methods) for the analysis of wind conditions, these differences were not significant.

In conclusion, I would like to emphasize that the purpose of nocturnal flights is very important for the study of completion of nocturnal migratory flights in passerines, apart from the temporal distribution of landings, fuel stores of the birds, and weather conditions. There is a reason to believe that some birds landing at night may have made night flights not directly related to the migration proper (cf. Mills et al. 2011; Taylor et al. 2011; Smolinsky et al. 2013). Further significant progress in understanding the causes of variations in the time of landing in the individual migrants might be possible when radio telemetry permits the tracking of birds for a long time. Currently, this is already technically possible not only for large- and medium-sized passerines (Cochran et al. 1967; Cochran and Kjos 1985; Cochran and Wikelski 2005; Mills et al. 2011; Smolinsky et al. 2013), but also for small passerines (Taylor et al. 2011).

ACKNOWLEDGEMENTS

I am most grateful to my colleagues Andrey Mukhin, Vladislav Kosarev, Dmitry Kishkinev, Arseny Tsvey for their assistance in the field. I thank the anonymous reviewer and Heiko Schmaljohann for many valuable remarks. The author acknowledges the British Atmospheric Data Centre (BADC) for providing wind balloon data. This study was supported by the Russian Foundation for Basic Research (grant 13-04-00242).

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