



Migratory stopovers of passerines in an oasis at the crossroads of the African and Indian flyways

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We studied migratory stopovers of nocturnal passerine migrants migrating between the Urals and Siberia and the Near East and Africa (five species) and between European Russia and the Indian subcontinent (two species) in an oasis in the arid belt of the northwestern edge of western Central Asia. In autumn, fuel loads of Blyth's Reed Warblers *Acrocephalus dumetorum* before their desert crossing were much greater than in Palaearctic–African migrants, which face a much narrower barrier, and also greater than in conspecifics captured during and after the desert crossing. However, another Indian migrant, the Red-breasted Flycatcher *Ficedula parva*, had low average fuel stores. In spring, Blyth's Reed Warblers carried less fuel than in autumn, and less than African migrants such as Garden Warblers *Sylvia borin* in spring. This suggests that the arid belt of western Central Asia is a serious ecological barrier for Palaearctic–Indian passerine migrants in autumn, but much less of one in spring. Palaearctic–African migrants which make a detour around this barrier to the northwest and migrate north of the Caspian Sea do not need large fuel stores like those they deposit before crossing the Sahara.

How birds cross ecological barriers is one of the most intriguing problems of bird migration research. Apart from large bodies of water, highlands and arid areas where no refuelling is possible may also be barriers for temperate-zone land birds. A number of studies have dealt with the migratory strategies of passerines crossing the Sahara (Bairlein 1985, 1988a, b, Biebach *et al* 1986, 1991, 2000, Biebach 1990, Biebach & Bauchinger 2003) and the deserts and highlands of western Central Asia (Dolnik 1982, 1985a, b, 1990, Bolshakov 2001). Studies in western Central Asia, including moon-watching and captures at stopovers, suggested the hypothesis that nocturnal passerine migrants breeding in Siberia and wintering in Africa avoid crossing the deserts in autumn; instead, they make a detour to the north and northwest and fly north of the Caspian Sea (Bolshakov 2001, 2002, 2003). This hypothesis is supported by moon-watching data from the northwestern edge of the desert north of the Caspian Sea (Bulyuk & Chernetsov 2005a, b).

We studied the stopover ecology of several common nocturnal passerine migrants in an artificial oasis on the northwestern edge of the arid belt, in the clay semi-desert north of the Caspian Sea. In both migratory seasons, the flyways of passerine migrants (i) flying from the Urals and Siberia towards the Near East and Africa and (ii)

flying from European Russia towards India and Pakistan cross in this area. Here, Palaearctic–African migrants in autumn face a relatively narrow belt of semi-desert in the trans-Volga and eastern Northern Caucasus. Even assuming that many of them make no stopover in the lower Volga, this barrier is not more than 500 km across, and a comparatively mild one. After crossing these (semi-)arid areas, African migrants get to the northern foothills of the Greater Caucasus or to the valleys of the Southern Caucasus where there are reasonable refuelling possibilities. Unlike Siberian–African migrants, European–Indian migrants north of the Caspian Sea start to cross the arid belt of western Central Asia, which offers very few refuelling options in autumn (Dolnik 1990). The distance to the northern foothills of the western Tien Shan, which is the closest good stopover area, is some 1,500–2,000 km (Fig 1). In spring, arid areas of western Central Asia offer significantly better stopover and refuelling possibilities to migrating passerines than in autumn due to the growth of ephemeral vegetation supporting an abundance of arthropods.

The aim of this study was to determine whether the main stopover parameters, *ie* duration of stay, energy condition at stopover, and refuelling rate, differ between passerines that stop over in the semi-desert north of the Caspian Sea and migrate towards Near Eastern and African winter quarters, on the one hand, and towards Indian winter

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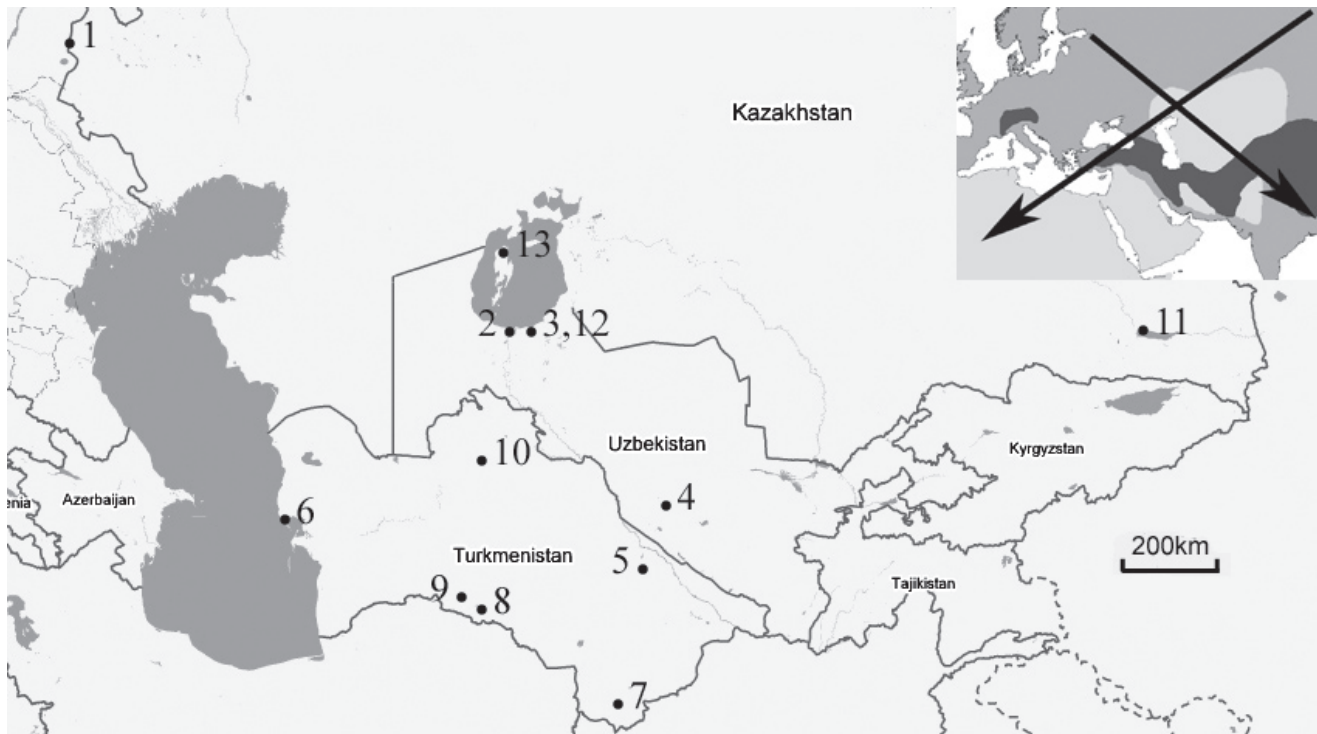


Figure 1. Map of western Central Asia and geographic position of the study site (site 1) and desert sites in Central Asia where Blyth's Reed Warblers were captured. For names of sites see Tables 4 & 5. In the upper right corner, the broader geographic framework is given. Arrows show the major flyways (the European-Indian and Siberian-African ones). Light grey colour represents arid areas, and dark grey represents highlands: both are potential barriers for migrating birds.

quarters, on the other. Apart from this, a comparison was drawn in several species between the condition of birds of different origin at spring and autumn stopovers. We aimed to establish the impact of environmental factors along the flyways on the condition of migrants before and after crossing arid regions.

METHODS

Study site

The study was carried out during the autumn migratory seasons of 2003 and 2004 and during spring passage in 2005 at the Dzhanibek field station of the Institute for Forestry, Russian Academy of Sciences (49° 24'N 46° 48'E). The field station is located on the border between the Volgograd region of Russia and the Western Kazakhstan region of Kazakhstan, in the clay semi-desert 375 km north of the Caspian Sea (Fig 1). The field station has a forest plantation of very diverse composition, including Pedunculate Oak *Quercus robur*, different maple species *Acer* spp., Horse Chestnut *Aesculus hippocastanum*, White Poplar *Populus alba*, Silver Birch *Betula pendula*, Ash *Fraxinus excelsior*, Red Ash *F. pennsylvanica* and many other species of trees and shrubs, including those carrying fruits: Rowan

Sorbus aucuparia, Single-seed Hawthorn *Crataegus monogyna*, Common Barberry *Berberis vulgaris*, Hedge Cotoneaster *Cotoneaster lucidus* etc. A more detailed description of the study area may be found in Karandina & Erpert (1972). This plantation has a total area of 10 ha and is an artificial oasis in semi-desert, which offers shelter and good foraging opportunities to both insectivorous and frugivorous passerine migrants. We also captured birds in a belt of windbreak forest in the vicinity which consisted of Siberian Elms *Ulmus pumila*.

Data collection

Mist-netting sessions were conducted during 3–18 September 2003, 22 August–7 October 2004, and 14–26 May 2005. The nets were permanently open, but the birds were only captured during daytime. The nets were inspected once per hour throughout the daytime period. Ringing protocol followed the specifications of the ESF project (Bairlein 1995), including the measuring of wing length and fat scoring. Birds were also weighed to the nearest 0.1 g. The overall length of mist nets was c150 m in 2003, c250 m in 2004 and 130 m in spring 2005.

We captured a total of 3,837 individuals of 38 species of passerine migrants. In autumn, four species of long-distance migrants (Common Redstart *Phoenicurus*

phoenicurus, Willow Warbler *Phylloscopus trochilus*, Garden Warbler *Sylvia borin*, and Red-breasted Flycatcher *Ficedula parva*) were captured in numbers sufficient for analysis of stopover duration, along with two medium-distance migrants (European Robin *Erithacus rubecula* and Chiffchaff *Phylloscopus collybita*). In spring, only two species were captured in appreciable numbers, Garden Warbler and Blyth's Reed Warbler *Acrocephalus dumetorum*. A possible reason is that the spring migration season was not completely covered by captures. Common Redstart, Willow Warbler, and Red-breasted Flycatcher probably passed through before the spring trapping session started. In autumn, the greater part of the migration season was covered by captures.

None of these species breeds at the Dzhanlybek field station or in its vicinity (Lindeman 1971). Therefore, all individuals captured may be considered transitory migrants. Common Redstarts and Willow and Garden Warblers winter in trans-Saharan Africa (Moreau 1972), Chiffchaffs probably spend their winter in the Near East and the eastern Mediterranean, and European Robins probably winter in the Southern Caucasus. All these species migrate in autumn through Dzhanlybek towards the southwest. Red-breasted Flycatcher and Blyth's Reed Warbler are Palaearctic-Indian migrants and fly in autumn towards the southeast, crossing the belt of deserts and highland of western Central Asia (Cramp 1992, Cramp & Perrins 1993).

Data analysis

We used Cormack-Jolly-Seber (CJS) models to estimate the probability of stay from the capture-recapture data (Lebreton *et al* 1992, Williams *et al* 2002). The CJS models estimate local 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 the stopover site at day $i+1$ (probability of stay, ϕ_i), as well as the probability that a marked individual that is present at the stopover site at day i is recaptured at day $i+1$ (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.

Stopover duration can be calculated from estimates of the probabilities of stay and seniority by simple transformations (Schaub *et al* 2001). We focus on the probability of stay only, because it was recently 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 $-1/\ln\phi_2$. Stopover duration of transients is one day, by definition. Motivation to proceed with migration and thus stopover behaviour of transients is quite different from behaviour of non-transients (Rappole & Warner 1976); thus we preferred to estimate the proportion of transients and stopover duration of non-transients, rather than to calculate the average stopover duration of transients and non-transients combined.

In autumn, the data from the two years (2003 and 2004) were analysed separately. The number of captures of Common Redstarts, Garden Warblers and Red-breasted Flycatchers was sufficient for analysis in both years; captures of Chiffchaffs, Willow Warbler and European Robin were sufficient only in 2004. A total of nine data sets were analysed using the MARK 4.0 program (White & Burnham 1999). We used Akaike's information criterion (AIC) to rank the models (Burnham & Anderson 1998). We evaluated the goodness-of-fit of models that did not account for transients using the program RELEASE implemented in MARK 4.0.

Fuel load was calculated by subtracting estimated lean mass, *ie* mass of birds with minimum fat score (0 by Kaiser 1993 scale), from the body mass of captured birds. Wing-length-specific lean body masses were calculated by linear regression (Bolshakov *et al* 2003). Condition index was expressed as body mass:wing length ratio (Safriel & Lavee 1988, Yosef & Chernetsov 2004, 2005).

RESULTS

Phenology of autumn passage

Phenological data refer to 2004, when trapping sessions covered most of the migratory period. Passage of Garden Warblers was recorded from first capture (22 August) until 3 October, with 90% of birds trapped before 19 September. On this day, the last wave of captures was recorded (24 individuals). Common Redstarts were trapped from first capture until 6 October; 90% were trapped by 3 October, *ie* passage continued until the end of our observations. Chiffchaffs were recorded throughout the

Table 1. Probabilities of stay (ϕ) and stopover durations of nocturnal passerine migrants in Dzhanlybek in autumn.

Species, year	Proportion of transients, τ	ϕ_1 mean and 95% confidence interval	ϕ_2 (or ϕ) mean and 95% confidence interval	Stopover duration (days) mean and 95% confidence interval
Garden Warbler* 2003	0.58	0.313; 0.182–0.482	0.746; 0.620–0.841	3.41 (2.09–5.77)
Garden Warbler* 2004			0.572; 0.443–0.693	1.79 (1.23–2.73)
Common Redstart* 2003			0.576; 0.383–0.748	1.81 (1.04–3.44)
Common Redstart* 2004	0.80	0.139; 0.080–0.231	0.684; 0.575–0.776	2.63 (1.81–3.94)
Chiffchaff** 2004			0.695; 0.564–0.800	2.75 (1.75–4.48)
Willow Warbler* 2004			0.307; 0.083–0.685	0.85 (0.40–2.64)
European Robin** 2004	0.65	0.215; 0.128–0.338	0.614; 0.424–0.774	2.05 (1.17–3.90)
Red-breasted Flycatcher*** 2003			0.712; 0.540–0.839	2.94 (1.62–5.70)
Red-breasted Flycatcher*** 2004	0.55	0.221; 0.109–0.396	0.490; 0.378–0.602	1.40 (1.03–1.97)

Notes: * long-distance Palaearctic–African migrant
 ** medium-distance migrant, wintering probably in the Near East and eastern Mediterranean
 *** long-distance Palaearctic–Indian migrant

Table 2. Body mass in autumn 2003–04 of passerine nocturnal migrants in Dzhanlybek. Body masses of birds that produced and did not produce recaptures are printed bold if the difference was significant and in italics if almost so (see text).

Species	Body mass, mean \pm SE, n	Estimated fuel load, % \pm SE	Body mass of birds subsequently recaptured, not recaptured, mean \pm SE, n	Body mass of birds subsequently recaptured, not recaptured, mean \pm SE, n
Garden Warbler*	20.16 \pm 0.087; 599	14.5 \pm 0.36 %	18.88 \pm 0.306; 43	20.26 \pm 0.090; 556
Common Redstart*	15.13 \pm 0.067; 564	11.4 \pm 0.38 %	14.21 \pm 0.265; 36	15.19 \pm 0.069; 528
Chiffchaff**	7.71 \pm 0.046; 344	8.7 \pm 0.48 %	7.72 \pm 0.253; 22	7.71 \pm 0.046; 322
Willow Warbler*	9.08 \pm 0.067; 276	13.0 \pm 0.55 %	8.53 \pm 0.711; 6	9.10 \pm 0.067; 270
European Robin**	15.12 \pm 0.036; 217	4.3 \pm 0.48 %	14.94 \pm 0.184; 25	15.14 \pm 0.085; 192
Blyth's Reed Warbler	14.21 \pm 0.348; 34	31.5 \pm 3.17 %	–	14.21 \pm 0.348; 34
Red-breasted Flycatcher*** 2003	9.74 \pm 0.052; 180	7.5 \pm 0.49 %	9.47 \pm 0.184; 16	9.77 \pm 0.042; 164
Red-breasted Flycatcher*** 2004	9.49 \pm 0.031; 569	5.4 \pm 0.30 %	9.27 \pm 0.117; 40	9.50 \pm 0.032; 529

Notes: see Table 1. No Blyth's Reed Warblers were recaptured at the site of ringing.

period of captures, but 90% of birds were trapped from 16 September when the first large influx occurred (18 individuals). Willow Warblers were trapped throughout the period of captures, with 90% recorded before 3 October. This means that intensive passage occurred throughout the period of study. Red-breasted Flycatchers were also captured throughout the trapping session, but 90% were trapped before 24 September. However, until the last day of captures 9–11 birds were trapped per day, *ie* passage remained rather intensive between 22 August and 6 October. Blyth's Reed Warblers were captured from the start of operations on 22 August until 27 September. European Robins were trapped between 16 September and 7 October 2004 (in 2003, the first bird was captured on 13 September), but 90% were captured from 27 September when the first wave of captures (10 birds) was also recorded.

Duration of autumn stopovers

In four data sets of the nine analysed (Garden Warblers in 2003, Common Redstart, European Robins and Red-breasted Flycatchers in 2004) the best model accounted for transients (Table 1). In such cases, we estimated probability of stay from the day of initial capture (ϕ_1) and probability of stay for the subsequent days (ϕ_2). In the five remaining cases, the best fit was achieved by the model with time-independent probabilities of stay (ϕ) and recapture probabilities (p).

The shortest stopovers were made by Willow Warblers (estimate 0.84 days, 95% confidence interval 0.40–2.64 days), the longest ones by non-transient Garden Warblers in 2003 (estimate 4.41 days, 95% confidence interval 3.09–6.77 days; Table 1).

Body mass of migrants in autumn

The only species with significant inter-annual difference in body mass was Red-breasted Flycatcher ($t_{747} = 4.18$, $P < 0.001$). In all other species the difference was not significant; therefore the pooled data are given (Table 2). Garden Warblers and Common Redstarts which were recaptured in the days subsequent to the initial capture, were (at first capture) significantly lighter than their conspecifics which were not recaptured ($t_{597} = 4.37$ and $t_{562} = 3.61$, respectively; $P < 0.001$). In Red-breasted Flycatchers in 2004 the difference was marginally not significant ($t_{567} = 1.92$, $P = 0.061$). In other cases, the difference was not significant. No Blyth's Reed Warblers were recaptured, so no data are available on this species (Table 2).

In most species, no age-related difference in body mass was recorded (Garden Warblers: $t_{431} = 0.76$, $P = 0.45$; male Common Redstarts: $t_{262} = 1.24$, $P = 0.22$; Willow Warblers: $t_{247} = 0.001$, $P = 0.999$; Red-breasted Flycatcher in 2003: $t_{178} = 0.73$, $P = 0.47$; European Robin: $t_{209} = 1.38$, $P = 0.17$). Only in 2004 were adult Red-breasted Flycatchers heavier than first-autumn birds (first-autumn: 9.45 g, SE = 0.032, $n = 505$; adults: 9.80 g, SE = 0.100, $n = 64$; $t_{567} = 3.43$, $P = 0.001$).

In 2004, body mass showed no calendar trend in Garden Warblers ($r_{433} = 0.05$, $P = 0.29$) and Willow Warblers ($r_{249} = 0.07$, $P = 0.30$), but increased through the season in Common Redstarts ($r_{459} = 0.15$, $P = 0.0006$), Red-breasted Flycatchers ($r_{568} = 0.27$, $P < 0.0001$), and Chiffchaffs ($r_{315} = 0.40$, $P < 0.0001$). Only in European Robins did body mass show a negative calendar trend ($r_{210} = -0.32$, $P < 0.001$). It should however be noted that a large portion of this species' passage period was not covered by captures (cf Lindeman 1971).

Body mass change during autumn stopovers

Mean mass change during stopovers in Dzhanybek was small in all species and varied from +0.20 g in Garden Warblers to -0.19 g in European Robins (Table 3). Mean daily mass change rate varied between +0.10 g.day⁻¹ in Common Redstarts and -0.11 g.day⁻¹ in Garden Warblers. The latter species had the highest overall mean mass change and the lowest mass change rate among all species studied. The reason was that many Garden Warblers that stopped over for a short time underwent rapid weight loss and individuals making longer stopovers gained mass. In this species the threshold stopover duration, after which

Table 3. Mass change and mass change rate of passerines migrants during autumn stopovers in Dzhanybek. If mass change was significantly related to stopover duration and initial body mass, the threshold is given. Mass change was positive when stopover duration was above the threshold and initial body mass below the threshold.

Species	Mean mass change, g ± SE	Mean mass change rate, g.day ⁻¹ ± SE	n	Threshold stopover duration, days	Threshold initial mass, g
Garden Warbler*	0.20 ± 0.202	-0.11 ± 0.065	72	1.3	20.3
Common Redstart*	0.16 ± 0.136	0.10 ± 0.082	64	0	15.7
Chiffchaff**	-0.02 ± 0.115	-0.02 ± 0.041	29	2.6	7.8
Willow Warbler*	0.08 ± 0.202	0.09 ± 0.107	11	-	-
European Robin**	-0.19 ± 0.090	-0.08 ± 0.047	52	-	-
Red-breasted Flycatcher***	0.04 ± 0.048	0.03 ± 0.032	123	-	9.5

Notes: see Table 1.

Table 4. Body mass of Blyth's Reed Warblers at different sites in deserts of western Central Asia during autumn passage.

Capture site	Geographic position	# in Fig 1	Body mass ± SE	n	Source
Dzhanybek, Kazakhstan	Before the barrier	1	14.21 ± 2.00	34	this study
Porlatau, southern Aral coast, Uzbekistan	Middle of barrier	2	12.4 ± 0.3	31	Yablonkevich <i>et al</i> 1991
Mau, southern Aral coast, Uzbekistan	Middle of barrier	3	13.2 ± 0.5	7	Yablonkevich <i>et al</i> 1991
Kuljuktai, Kyzyl Kum Desert, Uzbekistan	2nd half of barrier	4	10.9 ± 0.3	49	Lyuleeva & Lyuleev 1985b
Repetek, Turkmenistan	2nd half of barrier	5	11.6 ± 0.30	22	Bulyuk 1985
Ufra Peninsula, western Turkmenistan	After Caspian Sea crossing	6	10.1 ± 0.30	21	Bulyuk 1985
Murgab River, southern Turkmenistan, 1988	End of barrier	7	10.9 ± 0.4	4	Yablonkevich <i>et al</i> 1992
Murgab River, southern Turkmenistan, 1989	End of barrier	7	11.9 ± 0.2	25	Yablonkevich <i>et al</i> 1992

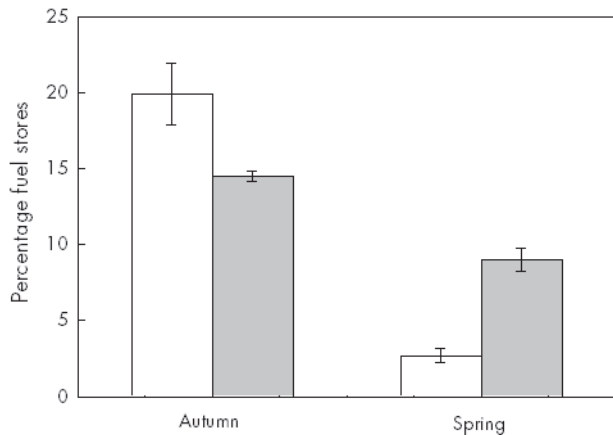


Figure 2. Fuel stores of Blyth's Reed Warblers (open bars) and Garden Warblers (filled bars) captured during autumn and spring passage in Dzhanlybek, western Kazakhstan (means \pm SE). Differences between species were significant: autumn, $t = 2.59$, $P = 0.014$; spring, $t = 7.20$, $P < 0.001$.

mass change became on average positive, was 1.3 days (Table 3).

The highest threshold duration of stay was in the Chiffchaff (2.6 days, Table 3), but it was smaller than the mean estimate of stopover duration in this species generated by the Cormack–Jolly–Seber models (Table 1). Thus, a considerable proportion of stopover migrants of each species gained mass during their stays in Dzhanlybek.

Spring migratory stopovers

The spring trapping session (14–26 May) was short and did not include a large part of the migration period. Passage of some species that were common in autumn but captured

in low numbers in spring (Chiffchaff, Willow Warbler, Common Redstart) mainly occurs earlier (Lindeman 1971). Only two species were trapped in numbers sufficient for analysis: Blyth's Reed Warbler and Garden Warbler. The low number of recaptures prevented us from estimating stopover durations. However, the fact that, of 110 Garden Warblers, none was recaptured in the days following the initial capture date (as against 43 of 599, 7%, in autumn) points to one-day stopovers being the norm.

Body mass of Blyth's Reed Warblers (11.30 ± 0.064 g; $n = 121$) and Garden Warblers (18.95 ± 0.168 g; $n = 102$) in spring after crossing arid areas was lower than in autumn (Table 2; $t = 13.5$, $P < 0.001$; $t = 5.34$, $P < 0.001$, respectively). Autumn mean body mass of Blyth's Reed Warblers exceeded their mean spring mass by 26%. In Garden Warblers, this difference was just 6%. Autumn fuel loads of Blyth's Reed Warblers were significantly higher than in Garden Warblers, whereas in spring the opposite pattern was observed (Fig 2). The mean condition index of Blyth's Reed Warblers in spring was 0.1794, SE = 0.0009, $n = 131$.

DISCUSSION

Of seven species included in the analysis, three (Garden Warbler, Willow Warbler and Common Redstart) were long-distance Palaearctic–African migrants, two (European Robin and Chiffchaff) were medium-distance migrants which probably winter in the Caucasus and the Near East, and two species (Red-breasted Flycatcher and Blyth's Reed Warbler) were long-distance Palaearctic–Indian migrants (Cramp 1992, Cramp & Perrins 1993). Species belonging to the two first groups migrate in autumn towards the

Table 5. Body mass of Blyth's Reed Warblers at different sites in the deserts of western Central Asia during spring passage.

Capture site	Geographic position	# in Fig 1	Body mass \pm SE	n	Source
Dzhanlybek, Kazakhstan	After the barrier	1	11.30 ± 0.70	122	this study
Kopetdag water reservoir, Turkmenistan	Beginning of barrier	8	10.1 ± 0.3	30	Yablonkevich <i>et al</i> 1985
Karakul, S Karakum Desert, Turkmenistan	Beginning of barrier	9	12.3 ± 0.23	12	Yablonkevich <i>et al</i> 1985
Murgab River, southern Turkmenistan, 1988	Beginning of barrier	7	11.0 ± 0.1	241	Yablonkevich <i>et al</i> 1992
Murgab River, southern Turkmenistan, 1989	Beginning of barrier	7	10.9 ± 0.1	570	Yablonkevich <i>et al</i> 1992
Kuljuktai, Kyzyl Kum Desert, Uzbekistan, 1973	First half of barrier	4	11.3 ± 0.3	25	Lyuleeva & Lyuleev 1985a
Kuljuktai, Kyzyl Kum Desert, Uzbekistan, 1981	First half of barrier	4	10.5 ± 0.2	125	Lyuleeva & Lyuleev 1985a
Shakh-Senem, N Karakum Desert, Turkmenistan	First half of barrier	10	12.9 ± 0.1	144	Yablonkevich <i>et al</i> 1985
Lake Sorbulak, near Alma-Ata, Kazakhstan	Eastern flyway	11	11.8 ± 0.1	410	Shimov 1985
Porlatau, southern Aral coast, Uzbekistan	Middle of barrier	2	12.6 ± 0.1	105	Yablonkevich <i>et al</i> 1991
Karateren, southern Aral coast, Uzbekistan	Middle of barrier	12	11.6 ± 0.1	58	Yablonkevich <i>et al</i> 1991
Barsakelmes, Aral Sea, Kazakhstan, 1982–83	Middle of barrier	13	12.0 ± 0.1	27	Yablonkevich <i>et al</i> 1985
Barsakelmes, Aral Sea, Kazakhstan, 1984	Middle of barrier	13	11.3 ± 0.1	212	Yablonkevich 1987

southwest, as suggested by their geographic distribution. Moon-watching data from Dzhanlybek in autumn suggest the existence of two distinct migratory directions: towards the southwest and towards the southeast (Bulyuk & Chernetsov 2005a, Bulyuk unpublished). Migrants towards the southwest face the relatively small ecological barrier of semi-deserts of trans-Volga and possibly Kalmykia (Fig 1). They are potentially able to stop over and refuel in the foothills of the Northern Caucasus. Blyth's Reed Warbler and Red-breasted Flycatcher migrate in autumn towards the southeast and face a wide arid belt which is followed by the highlands of western Central Asia.

Mean body mass of Blyth's Reed Warblers in Dzhanlybek was much higher than that of their conspecifics captured at different desert sites in western Central Asia and Kazakhstan (Table 4). The lowest mean values reported on the Ufra Peninsula on the Caspian coast (Table 4, site 6 in Fig 1) refer to birds captured after flights across the Caspian Sea. Comparison of data from Dzhanlybek on the northwestern edge of central Eurasia's arid belt with the data from the middle and southern part of this belt shows that, before crossing this barrier in autumn, Blyth's Reed Warblers take on large reserves of fuel (on average, 31.5%, Table 2). They are much larger than those put on by any other species in Dzhanlybek, eg by Garden Warblers which have the largest fuel loads among Palaearctic-African migrants but face a much smaller barrier (Table 2, Fig 2).

In spring, Blyth's Reed Warblers migrate from India and cross the desert zone towards the northwest (Bolshakov 2003). The mean mass of the birds after the desert crossing was not significantly different from mean mass before or during the crossing (Table 5). Blyth's Reed Warblers in spring in Dzhanlybek were in much better condition than Eurasian Reed Warblers *Acrocephalus scirpaceus* (0.1597, SE = 0.0004, n = 2,784, Yosef & Chernetsov 2005) and Sedge Warblers *A. schoenobaenus* (0.1497, SE = 0.0004, n = 2,146, Yosef & Chernetsov 2004) captured during spring passage in Eilat (southern Israel) after crossing the Arabian Desert. This strongly suggests that arid regions of western Central Asia offer long-distance passerine migrants much better refuelling opportunities in spring than in autumn.

Assuming that mean lean body mass of Blyth's Reed Warblers is 10.2 g (data from carcass analysis, Yablonkevich 1987), the mean fuel load of these birds in Dzhanlybek was 1.1 g, or 11%. It should be noted, however, that spring fuel loads of Blyth's Reed Warblers were lower than fuel loads of Garden Warblers that winter in Africa, approach Dzhanlybek from the southwest and cross no major barrier just prior to capture (Figs 1 & 2).

Red-breasted Flycatchers also winter in the Indian subcontinent, but unlike Blyth's Reed Warblers build up

no large fuel stores in autumn prior to desert crossing. Their mean body mass in Dzhanlybek in autumn (Table 2) was similar to the masses of birds captured in autumn in Turkmenistan after crossing most of the arid belt. In Repetek (eastern Turkmenistan, site 5 in Fig 1) the mean body mass of Red-breasted Flycatchers was 9.6 g (SE = 0.2, n = 22; Bulyuk 1985); on the Murgab River (southern Turkmenistan, site 7 in Fig 1) it was 9.9 g in 1988 (SE = 0.1, n = 127) and 9.4 g in 1989 (SE = 0.1, n = 55; Yablonkevich *et al* 1992). It cannot be ruled out that Red-breasted Flycatchers in autumn arrive at Dzhanlybek with low initial body mass and gain mass at low rates partly due to their foraging ecology: birds specialised in flycatching may have difficulty foraging when they carry large fuel loads. Similarly, the ecologically-similar Spotted Flycatcher *Muscicapa striata* does not gain much fuel before crossing the Sahara, unlike most other long-distance migrants (Schaub & Jenni 2000). A possible explanation is also that, with birds from the flycatcher family, sampling bias is stronger than in other groups. At migratory stopovers in Central Asia, mist-netted Spotted Flycatchers were significantly lighter than those shot by sporting guns (C.V. Bolshakov pers comm), ie birds carrying large fuel loads were under-represented in the mist-netting sample. However, a relatively large sample size of Red-breasted Flycatchers captured and recaptured by us (Table 2) suggests that sampling bias is unlikely as a complete explanation of the observed pattern.

Palaearctic-African migrants that face no major ecological barrier in Dzhanlybek in autumn (Common Redstart, Willow and Garden Warblers) have moderate body masses and fuel loads. The mean body mass of Garden Warblers (Table 2) and the proportion of birds with mass > 22 g (17%) is higher here than in most central European sites and lower than in most northern Mediterranean sites (Bairlein 1991). However, fuel loads carried by long-distance African migrants were somewhat heavier than those carried by medium-distance migrants (Chiffchaffs and European Robins, Table 2). It is worth noting that the body mass of most migrants shows no age-related variation. This suggests that the energy strategy of migration is similar in both adults and first-year birds.

Garden Warblers and Common Redstarts that were recaptured were significantly lighter at first capture than their conspecifics that were not recaptured. These two species increased their body mass during stopovers in Dzhanlybek more than others (Table 3). Apparently, species that on average carry significant fuel stores when captured (apart from the aforementioned ones, Willow Warbler and Blyth's Reed Warbler), gain them mainly before starting to cross the arid zone, probably in the forest-steppe where the availability of optimal habitats is much greater.

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