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Article

Tracking migration of black-headed buntings *Emberiza melanocephala* reveals the Iranian Plateau as an ecological barrier along the Indo-European flyway

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The black-headed bunting is one of the few species that migrate along the Indo-European flyway, and its migration routes and phenology are poorly understood. We provide the first individual-based year-round tracking study describing route choice and timing of black-headed buntings migrating from a breeding site in Croatia to a 6000 km distant non-breeding region in Maharashtra, central India. To evaluate landscapes important for the black-headed bunting migration, we quantified land covers and climates along the migration corridor. Stopover areas during the post-breeding migration were concentrated in four distinct regions: the Balkan Peninsula, central Anatolia, along with the Zagros mountain range and from the Indus river delta to the Kathiawar Peninsula. Post-breeding migration routes followed the shortest path connecting breeding and non-breeding sites, except for the initial detour from the breeding sites to the first stopovers at the Balkan Peninsula. The pre-breeding migration routes occur along the Arabian Peninsula, about 1000 km south of the post-breeding routes – creating a clockwise loop migration pattern. Post-breeding migration lasted about two months, whereas pre-breeding migration was almost two times shorter, conforming to energy- and time-minimisation strategies, respectively. During the post-breeding migration, birds seem to track ecological niches found on their breeding grounds. Post-breeding stopover areas were rich in mosaic lands and were in warm and dry climates of Mediterranean character, while forests and bare areas, as well as arid and humid climates, were avoided. Based on distinctly scarce and widely dispersed stopovers and high travel speeds over the Iranian Plateau along with prolonged stopovers before and after the Plateau, we identified the Iranian Plateau as a major ecological barrier for buntings and likely for other species migrating along the Indo-European flyway.

Keywords: light-level geolocation, long-distance migrant, loop migration, niche tracking, migration strategies



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Introduction

Migratory species often face hostile areas or obstacles along their migratory routes, referred to as ecological barriers, where fuelling opportunities are limited or absent.

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Birds usually have two options to overcome such barrier during the migration: either put on extra fuel load beforehand and engage in endurance flights to cross the barrier in a single leap, sometimes flying both during the night and day (Thorup et al. 2006, Adamík et al. 2016, Jiguet et al. 2019); or make a detour circumnavigating the barrier and fly shorter migration legs, stopping over at several sites which provide refuelling opportunities (Alerstam 2001, Léandri-Breton et al. 2019). The option of choice may vary between individuals and between seasons (Fraser et al. 2013, Deppe et al. 2015, Adamík et al. 2016), depending on a multitude of factors. Individual-based tracking can help to identify the extent of such ecological barriers and the strategies used to overcome them. It can also help to identify key stopover areas and environmental conditions that are relevant for the particular species.

Passerine migrants use intermediate stopover sites along the way for resting and refuelling when travelling between breeding and nonbreeding residence sites. Thus, a realised migration route is most likely adjusted to the spatial distribution of resources, potential migration barriers en route and individual flight capacity. Flight capacity is commonly related to deposited fuel, and fuel loads are strongly linked to the quality of resources along a migratory route (Lindstrom and Alerstam 1992, Weber and Houston 1997, Alerstam 2011). Availability of similar resources in various stages of the annual cycle is important for species that rely on and follow similar environments throughout the year – so-called ‘niche trackers’ (Nakazawa et al. 2004, Gómez et al. 2016). To evaluate relationships between the distribution of such species and environments globally, publicly available geographical layers such as land covers and climates may be used (Venier et al. 2004).

Most contemporary research on long-distance migration of Palaearctic passerines has been devoted to species of the western Palaearctic-African flyway (Briedis et al. 2020) and the Nearctic-Neotropical flyway (Faaborg et al. 2010). In contrast, the Indo-European flyway has received little attention except for a few recent tracking studies on bluethroats *Luscinia svecica svecica*, common rosefinches *Carpodacus erythrinus* and paddyfield warblers *Acrocephalus agricola* (Lislevand et al. 2015, Stach et al. 2016, Brlík et al. 2018, Lisovski et al. 2021), and thus data on the migration ecology of many species migrating along this flyway are still lacking. The Indo-European flyway encompasses the western part of the mid-latitude belt that divides the Eurasian plains from Africa, Arabia and India (Finlayson 2011). This region includes a series of geographical obstacles for landbirds such as the Black and the Caspian Seas, the Caucasus Mountains and the Hindu Kush mountains. The ridges and seas divide the Indo-European flyway into a northern branch, characterised by continental climate and associated forest and steppe vegetation, and a southern branch with prevailing warm (semi) arid and Mediterranean climates. Different species or populations might utilise one or both branches of the flyway. A recent study that integrated optimal migration modelling with geolocator tracking showed such a divide among different rosefinch populations (Lisovski et al. 2021).

In this study, we used light-level geolocators to track year-round movements of black-headed buntings *Emberiza melanocephala* from the western edge of the species breeding range. The black-headed bunting is an obligatory long-distance Indo-European migrant (Copete 2020) and a typical mid-latitude belt species. All life stages occur between 15° and 45°N with pronounced longitudinal distribution from 10° to 80°E (Copete 2020). The core breeding range encompasses the Levant, from the mid-Mediterranean to western Iran and from the Caspian to the Arabian Sea. Presently, there are only three ring recoveries linking breeding and potential non-breeding sites (Cramp and Perrins 1994, Balachandran et al. 2018, Croatian Ringing Scheme unpubl.), but further details on migration patterns are unknown. Here, we provide the first description of the spatio-temporal migration patterns of the species and identify key migration stopover regions. We infer species niche requirements by comparing the annual cycle locations of tracked birds to the distribution of land covers and climates. Further, we identify potential barriers for the species migrating along the Indo-European flyway.

Methods

Study area

The study population breeds in the region of Dalmatia, Croatia, and has reached densities of up to 34 singing males per km², as surveyed during the breeding season of 2010 (Barišić 2015). The core study area (43°50'N, 15°44'E) was in a shallow valley characterised by a high habitat heterogeneity with a small-scale mosaic of vineyards, olive groves, orchards, rain-fed cereal and vegetable fields surrounded and intersected with uncultivated fields in various stages of succession (garigue and macchia shrublands).

Field methods

During May/June 2014–2017, we captured 88 adult black-headed bunting males using mist-nets and playbacks. We focussed on males as they show high annual survival (up to 76% ± SE 3.6%, Kralj et al. 2016), are more conspicuous and considerably easier to catch than females. Mist-netting was done mainly during the short periods after dawn and before dusk to minimise disturbance and to avoid habituation of the birds to the nets. All birds were measured, weighed and ringed with the standard aluminium rings and a unique combination of three plastic colour rings – two rings on each tarsus.

We equipped 60 male buntings with geolocators (Fig. 1) – 10 per year in 2014 and 2015 and 20 per year in 2016 and 2017. The devices were fitted on the back of the birds using flexible leg-loop harnesses (Rappole and Tipton 1991) made from neoprene (2014), silicone (2015 and 2017) or non-flexible nylon cord (2016). All birds that were fitted with neoprene harnesses and returned to the breeding grounds in 2015 (n = 5) had lost the geolocators. These birds were dropped



Figure 1. The adult black-headed bunting males were equipped with the geolocators SOI-GDL2.0 and SOI-GDL2.1 (Swiss Ornithological Inst.). The geolocators, including stalk and harness, weighed between 0.62 and 0.70 g, which corresponded to approximately 2.0% (range 1.7–2.4%) of a male's body mass ($\bar{x}$ = 32.2 g, range 28.9–35.6 g).

from further calculations and the neoprene harness was inappropriate for future use. In addition, 28 males were captured, measured and ringed to serve as a control group ($n_{2014}=15$, $n_{2015}=5$, $n_{2016}=4$, $n_{2017}=4$). Geolocators recorded ambient light level starting from beginning/mid-July.

We recaptured 16 birds that returned with geolocators ($n_{2016}=3$, $n_{2017}=7$, $n_{2018}=6$). The difference in return rate between logger and control birds was insignificant in all years ($\chi^2 < 0.01$, $p=0.98$). Similarly, we found no significant differences in arrival to the breeding grounds between the two groups ($t=1.08$, $p=0.29$; Supporting information).

Geolocation analysis

Geolocators operated on 187 days on average (range 73–362 days). Four tags recorded the whole annual cycle while the others stopped recording from mid-September until late December ($\bar{x}$ = 18 Nov $\pm$ 28 days) due to shortage of storage space.

We used the threshold method to derive location estimates from the recorded light data. First, we log-transformed the recorded light values and defined sunrise and sunset times using the R-package 'TwGeos' by setting a

light-level threshold to one unit on the log-transformed scale (Lisovski et al. 2016). Second, we visually inspected the detected twilights and corrected the most obvious outliers by setting their time to the mean of the previous and the next twilight of the same type (sunset or sunrise). Further, we distinguished between movement and stationary periods applying the *invChanges* function from the R-package 'GeoLight' v2.01 (Lisovski and Hahn 2012). Based on this, we assigned twilight events to either movement or stationary periods (minimum duration = 3 days/6 twilight events). We then modelled individual migration tracks using the R-package 'SGAT' (Wotherspoon et al. 2016) which applies a Bayesian framework combining the observed sunrise and sunset data with a priori knowledge of bunting behaviour to provide location estimates with the associated uncertainty (Lisovski et al. 2020). This method allows refining the location estimates by combining the knowledge of the observed twilight error distribution (i.e. from calibration period), the plausible movement speed of the study species and species-specific spatial mask (e.g. land or sea). To this end, we used the 'group threshold model' with the pre-defined stationary and movement periods described above and allowed the birds to move in any direction but defined that stationary sites must be on land (i.e. land mask). The movement model was assumed to follow a gamma distribution (shape = 2.2, scale = 0.08), implying relatively few fast movements which would correspond to migration between the stopover sites. The twilight model was calibrated using sunrise and sunset times recorded while the bird was at the breeding site (in-habitat calibration; Lisovski and Hahn 2012). The resulting solar zenith angles ranged between 92.8 and 96.2 for individual birds. For the initial path, we extrapolated latitudinal positions during the equinox periods by setting the tolerance of solar declination of up to 9°. We initiated the model by drawing 1000 initial samples and then tuned the model a total of five times. Finally, we ran the model for 2000 iterations to ensure convergence and extracted median location estimates along with their 95% CIs.

Distribution of stopover sites, land cover and climate selectivity along the flyway

We defined the 'migration corridor' as the area encompassing 95% credibility intervals of all position estimates during the post-breeding migration, stopovers and movement periods, of all tracked birds combined (area of approx. 13.6 million km²) as inferred from the 'SGAT' analyses (above). First, we extracted the 100% CI corridor of each individual, then merged them in one and finally took 95% CI of the merged corridor. We used kernel density analysis to outline aggregations of median stopover estimates during the post-breeding migration into 'stopover regions'. Those regions were used for a spatial division of the migration corridor into 'migration zones' (below). The analysis was carried out using R-package 'adehabitatHR' (Calenge 2006). Bivariate kernels were calculated for all birds with the *kernelUD* function of 50%, with the smoothing parameter set to LSCV algorithm within the

interval 0.1–1.0, a resolution of 1000 pixels' grid and the extent to 0.2.

The black-headed buntings breed in a wide spectrum of chiefly Mediterranean habitats (Copete 2020). To test whether the black-headed bunting is a niche tracking migrant, i.e. whether it follows similar ecological conditions during the annual cycle, we analysed land covers and climates in stopover and residential areas identified with geolocators. First, we extracted land cover information within the migration corridor from the GlobCover 2009, Global Land Cover Map (ESA and UCLouvain 2010). In the migration corridor, we registered 21 land cover classes, merged structurally similar lands into six main land cover groups (croplands, croplands/natural vegetation mosaics, natural vegetation mosaics, forests, grasslands and bare areas); and excluded marginal land cover classes (<0.5% presence in the migration corridor), seas and freshwater bodies (Supporting information). Second, climatic data of migration corridor were

extracted from the Köppen–Geiger climate classification layer (Beck et al. 2018). We registered 20 climate classes in the migration corridor, combined climates according to their precipitation regimes into five main climate groups (desert, steppe, Mediterranean, humid and tropical), and excluded marginal climates (<0.5% presence in the migration corridor, see Supporting information). Third, we extracted land covers and climates within the 'stopover areas' that encompass the 95% confidence intervals around each stopover position (kite-like polygons, mean area per site = $59\,887\text{ km}^2 \pm 68\,652\text{ SD}$). For the known location of the breeding site, we buffered a 1° radius around the site ($38\,707\text{ km}^2$). Calculations were carried out in ArcGIS 9.3 (ESRI 2009). Finally, we checked for potential land cover or climate selectivity of migrating buntings by comparing land cover or climate composition in the migration corridor (available) to those at post-breeding stopover areas (likely occupied locations) with Manly's selection index (w_i) for Design 1 studies (Manly et al. 2002) using

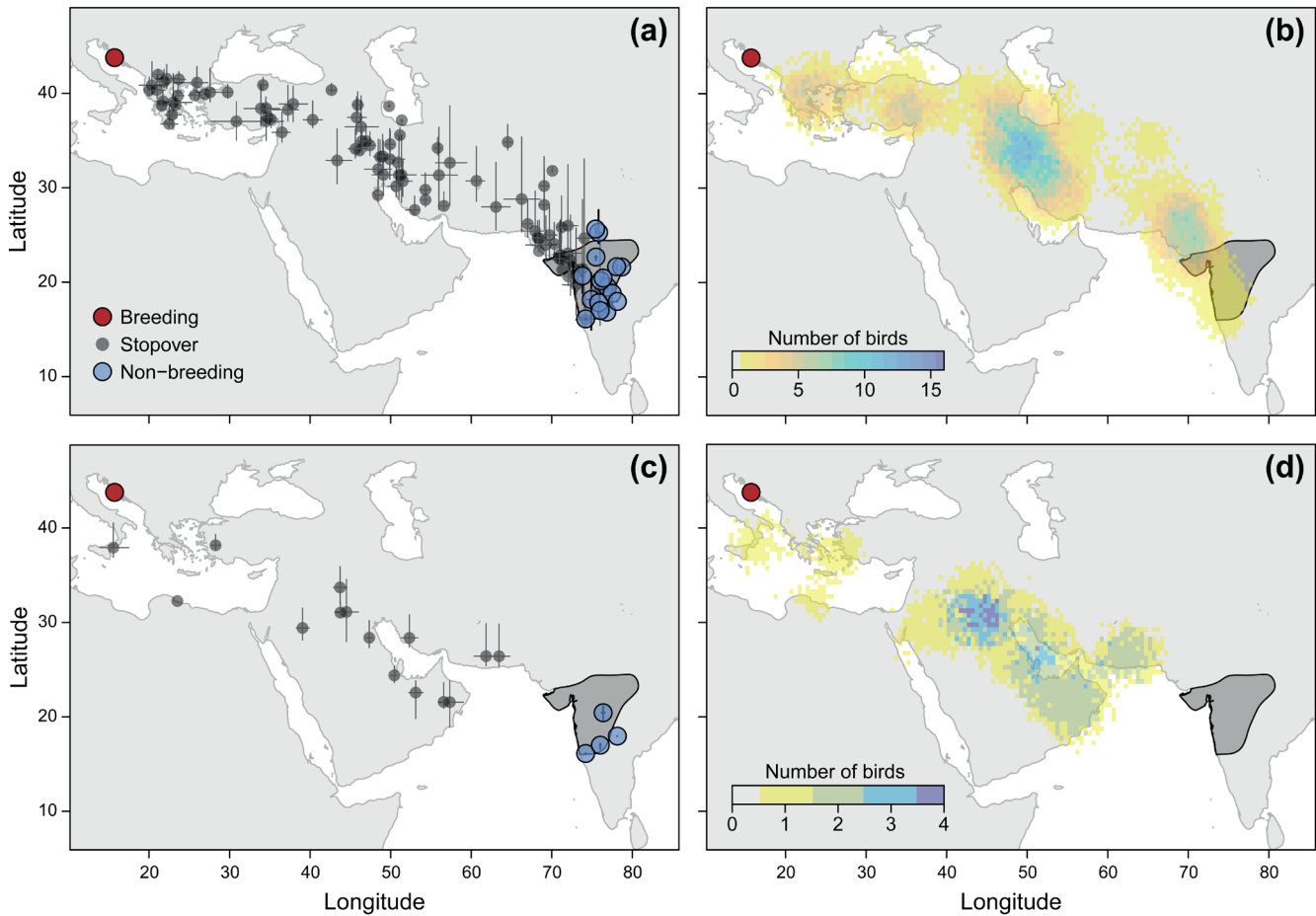


Figure 2. Post-breeding (a)–(b) and pre-breeding (c)–(d) migration patterns of black-headed buntings breeding in Croatia. Panels (a) and (c) show breeding site (red), stopover sites (grey) and non-breeding residences (blue) of all tracked birds ($n = 16$ for post-breeding migration and $n = 4$ for pre-breeding migration). Sites are shown with their 95% credibility interval of position estimates (thin grey lines). Panels (b) and (d) show site use by the tracked birds – the map was created by aggregating 90th quantiles of all position estimates between the start and end of the migration of each individual into a single raster. Thus, colour shows not only the number of individuals overlapping in space and but also where the individuals spent the most time during the migration (key stopover areas). The dark grey outline in all panels shows the assumed species non-breeding range (Copete 2020).

the R-package 'adehabitatHS' (Calenge 2006). Because the migration corridor encompassed various ecozones, which mainly changed longitudinally, we divided the migration corridor into 'migration zones' by using the longitudinal ranges of the stopover regions (kernel density analyses, see above) as boundaries. This resulted in seven migration zones, i.e. four stopover zones and three intermediate zones (Fig. 3a). We performed the zonal analysis by comparing land covers and climates in the migration corridor to those at the stopovers within a particular migration zone.

Results

Migration routes and stopovers

During the post-breeding migration, birds used on average six stopovers ($n=16$ birds, $n=93$ stopover sites) – four to nine stopovers per bird, with an average duration of 7.8 ± 6.3 days per stopover (Table 1). Most stopovers aggregated into four regions (83% of all stopovers): the Balkan Peninsula, the central Anatolia, the Zagros Mountain range and the region from the Indus River delta to the Kathiawar Peninsula (Fig. 3a, Supporting information). Stopovers in the intermediate zones were scarce, e.g. two in the western part of the Anatolian Peninsula, four in the zone encompassing upper courses of Tigris and Euphrates rivers and ten widely scattered stopovers over the Iranian Plateau.

Observed migration distances between the breeding site and the non-breeding residences were on average 334 km longer than the shortest – Great Circle – distances (5% detour; Table 1). Birds flew at $115^\circ \pm 22^\circ$ east-southeast directions without significant differences in directions between stopover regions (one-way ANOVA: $df=5$, $F=2.13$, $p=0.075$). However, we found a significant difference in bearing between the first and second migration leg (Bonferroni post hoc $p=0.04$) which corresponds to the apparent detour at the beginning of the trip ($125.5^\circ \pm 11.6^\circ$, Supporting information). It resulted in the stopovers being most distant from the shortest path in the Balkans (346 ± 145 km), and this disparity gradually decreased towards the east (312 ± 98 km in Anatolia, 281 ± 296 km in Zagros and 41 ± 294 km in Indus-Kathiawar).

Migration legs between consecutive stopovers averaged at 1092 ± 580 km. However, if the exceptionally long legs over the Iranian Plateau were excluded, legs averaged about 200 km less (890 ± 180 km), while those over the Iranian Plateau were twice as long (1974 ± 283 km). Distinct migration behaviour of birds over the Iranian Plateau was also evident in the movement speed – the speed of migration considering only movement period and excluding stopover time – which was 30.3% higher than elsewhere (468 ± 86 km day⁻¹ over the Plateau, 359 ± 18 km day⁻¹ elsewhere, Supporting information). Also, the average stopover duration before and after the Iranian Plateau was considerably longer than elsewhere (9.4 ± 3.1 days versus 4.4 ± 1 day).

During the pre-breeding migration, birds made 3–4 stopovers ($n=4$ birds, $n=15$ stopovers) and stopover duration

was 5 ± 1.8 days on average (Table 1). A key stopover region for all tracked birds was in the Mesopotamian plain, i.e. the plains of Euphrates and Tigris rivers in Iraq (Fig. 1d). Birds flew at a mean bearing of $303^\circ \pm 5^\circ$ west-northwest (Supporting information). Pre-breeding migration routes of all four birds were displaced further south compared to their post-breeding migration with the largest distances of about 1000 km (960 ± 396 km, 458–1581 km) in western Iran, the Iranian Plateau and the Arabian Peninsula. Thus, black-headed buntings migrated in a clockwise loop manner to complete their annual migration cycle.

Migration timing and the non-breeding residences

Birds departed from the breeding site around mid-July and arrived at their main non-breeding residences in mid-September, thus the post-breeding migration lasted roughly two months (Table 1 for exact dates). Duration of migration varied between individuals and the timing of departure from the breeding site and the arrival at the non-breeding residences were not correlated ($r=0.103$, $p=0.7$, $n=16$). The start of the pre-breeding migration averaged on the 1 April and the journey took 35 days on average – 55% less than the post-breeding migration period. Arrival at the breeding grounds (as inferred from geolocator data) was on average 6 May which was similar to the observed arrival of the tracked birds (4 May, the difference between arrival dates $t=-0.15$, $p=0.88$, $n=4$).

The non-breeding residences of all tracked birds were located in central India, mostly in the region of Maharashtra (Fig. 2, 3), over 6100 km away from the breeding site (Table 1). The distribution of individual residences shows birds did not share a common non-breeding residence but spread across a wider area (Fig. 2). As most loggers stopped working in Indian residences, the further seasonal comparison is based only on four loggers that recorded the full annual track. Compared to the post-breeding migration, during the pre-breeding migration birds had fewer stopovers (4 vs 5 ± 1) of shorter duration (5 ± 2 vs 10 ± 6 ; $t=4.15$, $p<0.001$, $df=14$), average movement speed (excluding stay at stopovers) was 99 km day⁻¹ faster (27%; $t=1.12$, $p=0.34$, $df=3$), and flight legs between the stopovers were 330 km longer (29%; $t=2.1$, $p=0.13$, $df=3$; Supporting information). The total distance travelled exceeded the post-breeding migration by 6% ($t=2.25$, $p=0.11$, $df=3$) and the total number of movement days was similar ($t=0.39$, $p=0.72$, $df=3$; Table 1). Birds spent on average 193 ± 3 days at their Indian non-breeding residences. Time spent at the non-breeding residences on average amounted to 54% of the annual cycle, breeding period – 20%, post-breeding migration – 16% and pre-breeding migration – 10%.

Land covers and climates selectivity

The breeding site and non-breeding residences were characterised by either croplands with natural vegetation mosaics (57% each) or pure croplands (31% and 41%

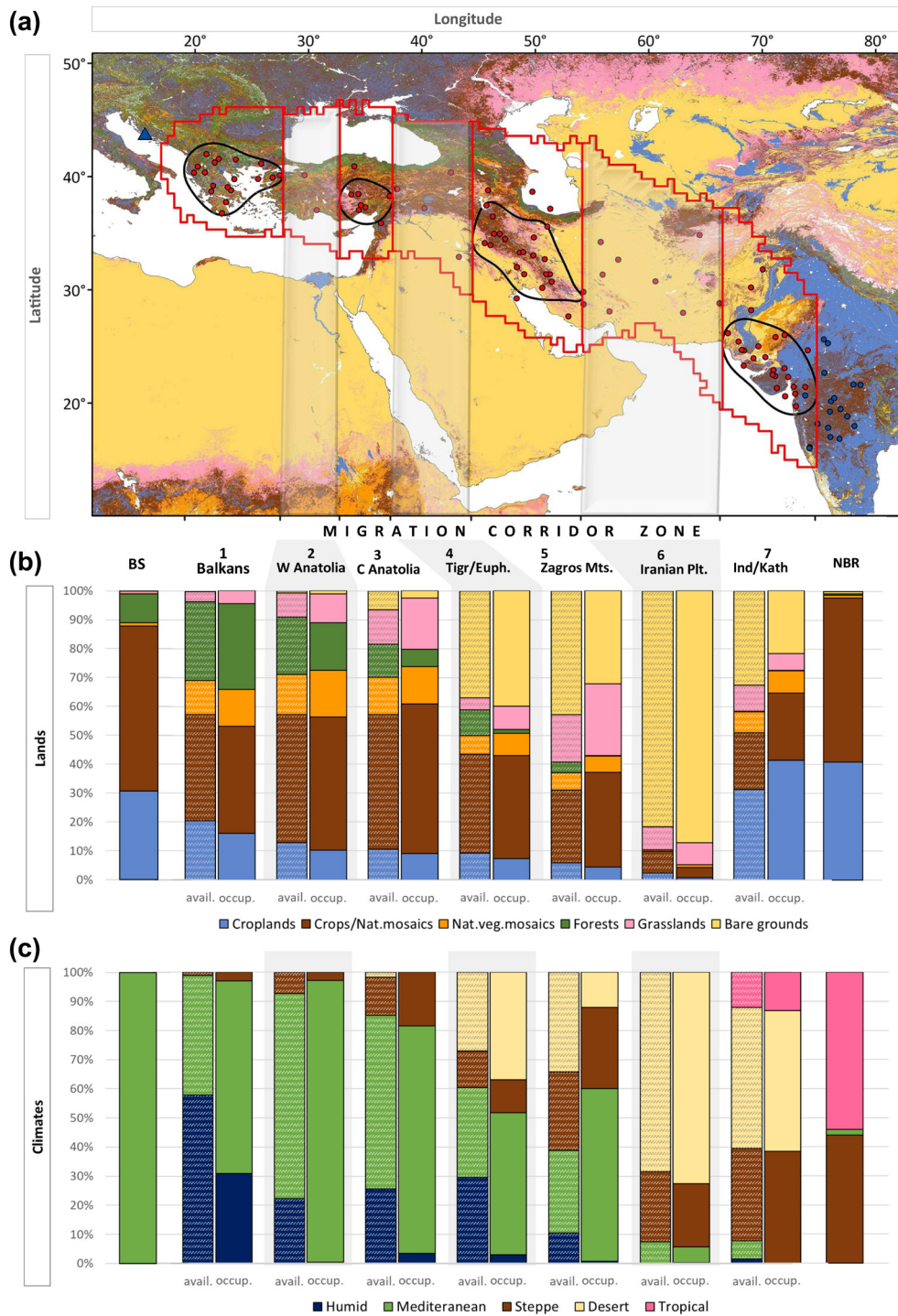


Figure 3. Area occupancy of black-headed buntings during the post-breeding migration and non-breeding residency. (a) Median estimates of post-breeding stopover sites are shown as red dots and non-breeding residences as blue dots; the breeding site is depicted as a blue triangle. The background map shows major land cover groups (ESA and UCLouvain 2010). Stopovers clustered in four major stopover regions (black-lined polygons – 50% probability kernels). Migration corridor (red-lined polygon) is sliced into seven migration zones: four stopover zones (1 – Balkans, 3 – central Anatolia, 5 – the Zagros Mountains, 7 – Indus River-Kathiawar Peninsula) and three intermediate zones (2 – western Anatolia, 4 – upper Tigris-Euphrates, 6 – Iranian Plateau; shaded areas in the map). (b) The proportion of land covers at the likely occupied areas (1° buffered breeding site, 95% CI buffered stopovers and 95% CI buffered non-breeding residences) compared to the proportion of land covers available (slightly transparent) along the migration zones (intermediate zones are shaded). (c) The proportion of climates at the likely occupied areas (1° buffered breeding site, 95% CI buffered median stopovers and 95% CI buffered non-breeding residences) compared to the proportion of climates available (slightly transparent) along the migration stopover zones and intermediate zone of the Iranian plateau (intermediate zones are shaded).

Table 1. Summary data of the post-breeding and pre-breeding migration of black-headed buntings equipped with light-level loggers in Croatia 2014–2017.

Event	Post-breeding migration (n=16) $\bar{x} \pm \text{SD}$ (range)	Pre-breeding migration (n=4) $\bar{x} \pm \text{SD}$ (range)
Onset	17 Jul $\pm$ 6 d (5–26 Jul)	1 Apr $\pm$ 1 d (30 Mar–2 Apr)
End	18 Sep $\pm$ 8 d (30 Aug–29 Sep)	6 May $\pm$ 3 d (2–9 May)
Duration (days)	64 $\pm$ 9 (45–78)	35 $\pm$ 3 (30–37)
Trip distance		
Travelled (km)	6490 $\pm$ 300 (6143–7324)	6912 $\pm$ 204 (6668–7098)
Great Circle distance (km)	6156 $\pm$ 228 (5697–6445)	6296 $\pm$ 134 (6127–6445)
Number of stopovers	6 $\pm$ 1 (4–9)	4 (3–4)
Days stationary		
Average at a stopover (d)	7.8 $\pm$ 6.3 (1–36)	5 $\pm$ 1.8 (2.4–8.5)
Cumulative total (d)	44.3 $\pm$ 8.9 (25.9–56.3)	18.7 $\pm$ 2 (16.4–21.2)
Days on move		
Average between 2 stops (d)	2.7 $\pm$ 1.6 (1.3–8.3)	3.5 $\pm$ 2 (1.4–8.7)
Cumulative total (d)	19.4 $\pm$ 4.9 (12.7–31.8)	17.4 $\pm$ 5.8 (13.3–26.0)
Distance between 2 stops (km)	953 $\pm$ 544 (181–2503)	1457 $\pm$ 650 (452–2753)
Speed (while moving) (km day ⁻¹)	364 $\pm$ 140 (124–836)	461 $\pm$ 167 (228–896)

respectively; Fig. 3b). Those lands were the main vegetated lands within the migration corridor too, but less abundant (36%; Supporting information). The remaining vegetated lands belonged to an array of natural vegetation mosaics, grasslands and forests (22%). The overall dominant land cover within the migration corridor were bare areas (42%). Their presence increased eastwards along the corridor from being almost absent in the Balkan Peninsula to the maximum of 82% at the Iranian Plateau (Fig. 3b, Supporting information). At the post-breeding stopover areas, buntings occupied lands non-randomly (Manly's test $\chi^2 = 295.411.0$, $df = 5$, $p < 0.001$), indicating selectivity of croplands and grasslands as well as avoidance of forests and bare grounds (Table 2). Among vegetated lands, the most abundant land cover at stopover areas were croplands with natural vegetation mosaics (Table 2, Supporting information).

The climate at the breeding site was the Mediterranean, while the non-breeding residences in India were equally distributed between steppe and tropical climates characterised by dry and warm winters (September–February) and hot summers (March–May; Fig. 3c). Mediterranean and humid climates were most abundant in the western part of the migration corridor, while the eastern part was dominated by desert and steppe climates (Fig. 3b, Supporting information). Stopover areas during the post-breeding migration were non-randomly distributed in climates ($\chi^2 = 1144.452.0$, $df = 4$, $p < 0.001$), indicating that tropical, Mediterranean and steppe climates were favoured, while humid and desert climates were avoided (Table 2). Tropical climates were exclusively (and scarcely) present only in the easternmost zone (Fig. 3c, Supporting information).

During the pre-breeding migration (n=4), stopover areas were predominantly covered with bare lands (83%), while

Table 2. Manly's (design 1) non-standardised indices (w_i) showing selectivity indices for land covers and climates during the post-breeding migration of black-headed buntings breeding in Croatia: in the whole migration corridor, stopover migration zones and intermediate zone of the Iranian Plateau. Sample units were surfaces (km²) taken from the Global Land Cover Map (ESA and UCLouvain 2010) and the Köppen–Geiger climate classification layer (Beck et al. 2018). Likely occupied lands and climates of stopover areas were extracted from polygons encompassing 95% confidence intervals of median stopovers, available lands and climates were all lands and climates present within the migration corridor in a proportion larger than 0.5% (Supporting information). Scores in the table, presenting the selection indices, are ratios between proportions of likely occupied locations and available resources. Selection indices above 1.0 indicate a preference, those less than 1.0 indicate avoidance.

Resources	All zones	Balkan Peninsula	Central Anatolia	Zagros Mts	Iranian plateau	Indus-Kathiawar
Land covers						
Croplands	1.34	0.80	0.87	0.77	0.35	1.33
Crops/Nat. mosaics	1.08	1.01	1.11	1.30	0.49	1.16
Natural veg. mosaics	1.11	1.07	0.99	0.94	1.83	1.08
Forests	0.56	1.09	0.52	0.04	0	0.37
Grasslands	1.33	1.23	1.49	1.50	0.94	0.64
Bare areas	0.84	0.73	0.38	0.75	1.07	0.67
Climates						
Desert	0.92	–	0.00	0.35	1.06	1.00
Humid	0.24	0.53	0.13	0.06	4.06	0.02
Mediterranean	1.35	1.61	1.31	2.09	0.73	0.00
Steppe	1.23	2.79	1.41	1.04	0.91	1.21
Tropical	1.93	–	–	–	–	1.09

vegetated lands at stopover areas belonged mostly to grasslands (7%) and croplands with natural vegetation mosaics (6%). Most stopover areas were dominated by desert climates (82%), except from the westernmost stopovers which were in the Mediterranean climates (12%).

Discussion

We provide the first description of the year-round spatial and temporal distribution of migratory black-headed buntings. Furthermore, we identify the area of the Iranian Plateau as a major ecological barrier on their migration route. Hitherto, buntings were assumed to depart from the breeding grounds in late July–August and arrive at the non-breeding residences in late August and September (Copete 2020). Our tracking data now reveals a longer post-breeding migration period lasting for about two months until mid-September. Further, our data from the pre-breeding migration of four birds largely confirm the earlier observation-based assumption of a pre-breeding migration period starting in March–April (Copete 2020). We show that black-headed buntings pass through the Arabian Peninsula during the pre-breeding migration, a region where the species is regularly observed in low numbers (Stresemann 1944, Cramp and Perrins 1994).

On a sample of four birds, our study emphasised the differences between the post-breeding and the pre-breeding journeys regarding the migration duration, the total length of the trip and the length of individual stopovers and migration legs. For instance, the pre-breeding migration lasted 29 days less, despite the 6% longer migration distance. This suggests that buntings likely conform to an energy minimisation strategy during the post-breeding migration but to a time minimisation strategy during the pre-breeding migration – a common pattern among many migratory species (Gudmundsson et al. 1991, Alerstam 2011). Selective pressure for early arrival at the breeding grounds has been theoretically outlined as a determinant for fast pre-breeding migration (Kokko et al. 2006). Annual migration routes of tracked buntings resulted in an ellipsoid clockwise loop pattern, with the pre-breeding migration routes situated more to the south from the post-breeding routes. Looped migration may indicate seasonally different migratory constraints or opportunities en route. A similar loop migration pattern has been described frequently for passerines, for instance, in the nightingale *Luscinia megarhynchos* (Hahn et al. 2014), the great reed warbler *Acrocephalus arundinaceus* (Lemke et al. 2013) and the barn swallow *Hirundo rustica* (Briedis et al. 2018) along the African-European flyway, and in the common rosefinch *Carpodacus erythrinus* along the Indo-European flyway (Stach et al. 2016, Lisovski et al. 2021). Black-headed buntings are protandric migrants (Cramp and Perrins 1994) and, as we tracked only males, further studies of females should examine whether the observed migration pattern applies to females and verify the scope of sex-specific differences in migration strategies.

Our analysis showed that buntings inhabit areas in dry and warm or hot climatic conditions in heterogeneous landscapes during all stages of their annual cycle, suggesting they should be considered as niche tracking migrants. Niche tracking behaviour has been found in many passerine migrants (Martínez-Meyer et al. 2004, Nakazawa et al. 2004, Gómez et al. 2016). At the breeding grounds, buntings inhabit an array of structurally different environments, from semi-open grasslands and arable lands to semi-closed degraded forests but in predominantly Mediterranean climates, suggesting their land cover niche is broader than the climatic one. Similarly, during the post-breeding migration, buntings predominantly likely stayed in Mediterranean climates and although they avoided forests and bare areas, we did not find a strong preference for any specific land cover group. Such a plasticity in selection of landscapes may be an adaptation of small-sized Passerine migrants to compensate for the vulnerability of small body size to alternating environmental conditions and lower flight capacities (Cresswell 2014). Availability of heterogeneous mosaic land covers and Mediterranean climates was the highest in its western part of the migration corridor from the Balkans to Zagros Mts, coinciding with the core breeding range of the black-headed bunting. Therefore, with respect to the patchiness of suitable environments and their temporal variability, it can be argued that black-headed buntings have good availability of suitable environments to ensure migratory refuelling en route during the first part of their post-breeding migration. Expanding on this argument, a rather consistent length of migration legs of ca 900 km in this section of the migration corridor potentially refers to the preferred distance of a single migration leg of the species.

At the broad geographical scale, suitable environments are distributed in the longitudinal direction, funnelled by seas, deserts in the south and mountains in the north. Our analysis suggests that birds mainly avoided forests and humid climates as well as bare areas associated with desert climates. Avoidance of the first explains the uniform initial detour from the shortest path to the Balkan peninsula, while avoidance of the former sheds light on a variety of individual migratory behaviours over the Iranian Plateau. The stopover area at the Balkan peninsula was a major deviation from the shortest great circle route. By making this detour, buntings avoided unsuitable forested areas in humid and cold continental climates of the Dinaric Alps, where Mediterranean habitats are scarce. It seems a reasonable trade-off to take a slightly longer migration route but potentially avoid unsuitable habitats. On the other hand, this detour could have historic origins owing to the species' range expansion from the Balkans into the eastern Adriatic coast. Such historically based detours have been suggested in several species travelling along the Afro-Palearctic flyway, e.g. red-backed shrike *Lanius collurio* (Tøttrup et al. 2017), marsh warbler *Acrocephalus palustris* and lesser whitethroat *Sylvia curruca* (Sutherland 1998).

At the Iranian Plateau, migrating buntings showed exceptional behavioural patterns compared to the rest of the post-breeding migration. The Iranian Plateau, between the Zagros

mountains and the Indus-Kathiawar stopover region, is an area of almost 4 million km² characterised by arid climates and scarce vegetated lands (Fig. 3a). These characteristics considerably deviated from the rest of the migration corridor. Here, individuals stopped over rarely and for short periods only. On the contrary, before and after the plateau birds made longer stopovers than elsewhere stopping for ca seven days in Zagros Mts and ca 12 days in the Indus-Kathiawar region compared to four to five days long stopovers in the Balkans and central Anatolia (Supporting information). Long stopovers before and after crossing the plateau might show extensive fuelling – a typical pattern in migrating passerines when dealing with an ecological barrier (Fransson et al. 2008, Lemke et al. 2013, Briedis et al. 2016, Blackburn et al. 2019). Buntings crossed the plateau with 30% higher travel speeds than elsewhere, covering ca 2000 km in just four days (Supporting information). Several geolocators recorded full light patterns (Supporting information) over the Iranian Plateau. Although full light patterns alone could be explained by other factors, such as lack of vegetation at a stopover, high travel speed in conjunction with full light patterns recorded over the Plateau suggest prolonged nocturnal flights into the day, a strategy that nocturnal migrants utilise when overcoming the Sahara desert along the African-Palaeartic flyway (Adamík et al. 2016, Ouwehand and Both 2016, Jiguet et al. 2019). Scarce and widely dispersed stopover sites, prolonged stopovers prior and after and high travel speed all suggest that the Iranian Plateau is a major migration barrier along the Indo-European flyway for the black-headed bunting. Only recently, several ecological barriers have been identified along the Indo-European flyway via theoretical optimisation modelling (Lisovski et al. 2021) and our results suggest a further, previously unknown barrier for black-headed buntings.

The pre-breeding migration tracks were of the much smaller sample size compared to the post-breeding period, but all four individuals made a rather uniform southward shift and passed through seemingly inhospitable areas as most stopovers were found in areas covered by bare ground and desert climates – environments avoided during the post-breeding migration. However, during the pre-breeding migration, lands around the Persian Gulf and the Middle East are in the period of climatic spring transition (April–May), characterised by the end of (winter) rains and a gradual increase of temperature. This supposedly generates conditions for vegetation growth that ensure enough refuelling resources en route in April. Also, it might be that black-headed buntings on pre-breeding migration gain support from favourable wind conditions over the Arabian Peninsula (Lisovski et al. 2021). Our pre-breeding inferences were drawn from only four birds, thus future efforts in the research of black-headed bunting migration should focus on this period of the annual cycle.

Information about phenology and migration routes of black-headed buntings preceding this research was scarce. Without prior expectations, we identified not only key stopover regions but also the major barrier to post-breeding migration. Approximately two-thirds of the post-breeding migration route of the Adriatic black-headed buntings went

through likely hospitable areas of the species' breeding range until the birds reached the Iranian plateau. Biotic and abiotic characteristics of the Iranian Plateau make this area hostile for the buntings and birds changed their migration strategy upon reaching the Plateau. Similar to the deserts of central Asia for the Siberian-Indian flyway and the Sahara Desert for the Afro-Palaeartic flyway, the Iranian Plateau most likely represents the major ecological barrier along the southern branch of the Indo-European flyway providing little fuelling opportunities not only for the black-headed bunting but also for other migratory birds.

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Davor Ćiković: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Sanja Barišić:** Conceptualization (equal); Formal analysis (supporting); Investigation (lead); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Steffen Hahn:** Software (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Vesna Tutiš:** Investigation (supporting); Writing – review and editing (supporting). **Jelena Kralj:** Investigation (supporting); Writing – review and editing (supporting). **Martins Briedis:** Formal analysis (supporting); Software (lead); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability statement

The bird tracking dataset is available from Zenodo open data repository: <<https://doi.org/10.5281/zenodo.5541288>> (Ćiković et al. 2021) and available upon request from the Movebank online database (<<https://www.movebank.org/>, project ID: 1751686690>).

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