Communication

Regional wind patterns likely shape a seasonal migration detour

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Migrating animals should optimise time and energy use when migrating, travelling directly to their destination. Detours from the most direct route may arise however because of barriers and weather conditions. Identifying how such situations arise from variable weather conditions is crucial to understand population response in the light of increased anthropogenic climate change. Here we used light-level geolocators to follow Cyprus wheatears for their full annual cycle in two separate years migrating between Cyprus, over the Mediterranean and the Sahara to winter in north–east sub-Saharan Africa. We predicted that any route detours would be related to wind conditions experienced during migration. We found that spring migration for all birds included an eastern detour, whilst autumn migrations were direct across the Sahara. The direct autumn migration was likely a consequence of consistent tail-winds, whilst the eastern detour in spring is likely to be more efficient given the wind conditions which are against a direct route. Such variable migration routes shaped by coincidence with prevailing winds are probably common suggesting that some birds may be able to adapt to future changes in wind conditions.

Keywords: bird migration, geolocator, loop migration, migration detour, wind

Introduction

Migration allows animals to track seasonally variable resources (Alerstam et al. 2003, Thorup et al. 2017), and migration routes often vary between seasons as resources and environmental conditions are also highly variable in space and time (Tøttrup et al. 2017, Briedis et al. 2018a). These different routes have been linked to wind conditions (Vansteelant et al. 2017) and seasonally variable environmental conditions (Stach et al. 2016), but may also arise because of the distribution of suitable habitat (Hahn et al. 2014). Consequently, it is crucial to understand how migration routes arise in response to weather, barrier and habitat variation particularly in the light of current and future anthropogenic environmental and climate change.

Migrating animals should minimise time and energy of migration (Hedenstrom and Alerstam 1997) and for birds, wind assistance may be very important in this. Global wind patterns, for example, help to shape migration routes (Shamoun-Baranes et al. 2017), particularly in birds, so that they tend to migrate through flyways that optimise favourable wind conditions to increase migration speed and survival, rather than following the most direct great-circle route (Erni et al. 2005, Kranstauber et al. 2015).

They can also time their migration departure to coincide with tailwinds (wind selectivity) (Able 1973, Akesson and Hedenström 2000), travel at altitudes that maximise wind support (Mateos-Rodríguez and Liechti 2012, Senner et al. 2018) and compensate for wind drift (McLaren et al. 2012). Some bird species demonstrate lower wind selectivity however, where efficient foraging opportunities at stop-overs are unavailable (Thorup et al. 2006) and where there is a cost to late arrival on the breeding (Nilsson et al. 2014) or non-breeding ground (Ward et al. 2018).

Climate change may influence wind patterns and these could have both positive and negative effects on migratory species (La Sorte et al. 2019). In some areas, supportive winds have increased in regularity over time, presumably having a positive effect on flying conditions for migrant birds (Gordo 2007). Where regular wind patterns change negatively though, migrating birds could expend more energy during migration and in some cases migration routes could be lost (Nourani et al. 2017) or rerouted (Eisaguirre et al. 2018), whilst delayed arrival to the breeding grounds could exacerbate ecological mismatch and impact population trends through reduced survival and lower productivity. Determining how migration strategies relate to en route wind conditions is therefore important in understanding how changes to wind patterns may affect migrant bird populations.

Here we use light-level geolocation data from 13 adult Cyprus wheatears *Oenanthe cyprica* to investigate seasonal variation in migration route in order to further understand the role of wind conditions. We predicted that migration routes would be direct (note that great-circle and rhumb line routes are virtually identical in this system), but that any deviations from this can be explained by wind variation as birds follow supportive winds.

Methods

Study site and capture of birds

Cyprus wheatears are small obligate migrants, which migrate from their breeding range in Cyprus to eastern sub-Saharan Africa. We tagged 24 adult (12 females and 12 males) Cyprus wheatears in 2014 (Xenophontos et al. 2017) and 47 adults (24 females and 23 males) in 2017 at the National Forest Park of Troodos (NFP of Troodos; 34°56′11″N, 32°51′48″E). Birds were captured throughout the breeding season from May through to August using mist nests and spring traps in combination with conspecific playback. Each bird was individually identified with a unique combination of four colour-rings that included a metal ring provided by BirdLife Cyprus. In 2014 an additional 78 birds (36 females and 42 males) were colour-ringed but untagged, and another 59 (21 females and 38 males) in 2017 for analysis of tag effects on return rates.

Data from the birds tagged in 2014 were reported in Xenophontos et al. (2017), but this only considered the autumn migration. Here we include the spring migration for those tagged birds and an additional year of data for

replication. In 2017 we fitted geolocators following that same methods as in Blackburn et al. (2016) and Xenophontos et al. (2017). We deployed Biotrack ML6740 Mk6 geolocators with 5 mm light stalks fixed at an angle 45° and used legloop harnesses made from 0.8 mm diameter transparent elastic cord (Rappole 1991). The mean combined weight of the harness and tag was 0.60 ± 0.01 g [mean $\pm 1 \times$ SD] whilst the mean bird mass was 16.3 ± 1.5 g [mean $\pm 1 \times$ SD]) (range: 3.0–4.6% of the bird's weight). Harnesses were attached to geolocators prior to fitting to birds and the fitting process took approximately 1 min.

In 2015 the return rate of tagged birds (58.3%) was very similar to that of colour-ringed only birds (55.6%): $X^2 = 0.001$, $p = 0.99$. In 2018 fewer tagged birds (27.7%) than colour-ringed only (47.5%) returned to the field site although this difference was not statistically significant: $X^2 = 1.465$, $p = 0.23$. We suspect that the differences in return rates between years relate to the site fidelity of first year adult males in the pre-breeding period, where some adult males in 2017 were tagged before they had settled in a territory (this was only apparent later in the field season) and so some of these birds were likely to have moved beyond the field site. The return rates of tagged female birds in 2018 (34.8%) was similar to colour-ringed only birds (38.1%): $X^2 = 0.001$, $p = 0.99$, whilst fewer tagged males were resighted (21.8%) compared to the colour-ringed only group (53.8%): $X^2 = 1.93$, $p = 0.16$.

Geolocators data analysis

Raw data were downloaded using BAStrack decompressor software (British Antarctic Survey, Cambridge, UK) and we adjusted for clock drift, assuming that any drift was linear. Further processing and analysis was carried out in R (<www.r-project.org>). Twilights were defined using the BAStag R package (Wotherspoon et al. 2016) and a threshold of 2. Outliers that were likely caused by shading were identified using the LoessFilter function in the R package Geolight (Lisovski and Hahn 2012) with $K = 5$ interquartile ranges. Between 2 and 18 twilights were identified as outliers in 9 of the 13 tags and were removed from analysis. Summer sun elevation angles (SEAs) were obtained over the breeding period where birds were at a known location (i.e. Troodos) resulting in SEAs ranging from −4.02 to −3.24 degrees. Winter SEAs were estimated for each bird using the Hill–Ekstrom calibration (Hill and Braun 2001, Ekstrom 2004, Lisovski and Hahn 2012) over a stationary period of 30–90 days between the 15th of November and 31st of January resulting in SEAs ranging from −6 to −2.5 degrees. Estimation of one summer and two winter SEAs failed and so the median value for the respective year and season was used in these cases. Coordinates were produced for each twilight using the 'coord' function in the Geolight package. Latitude estimates were ignored for two weeks either side of the spring and autumn equinoxes, and since spring migration occurs close to and during the spring equinox we rely primarily on longitude estimates and time in our analysis. Timing of migration was estimated by

visual identification of sudden consistent changes in sunrise and sunset times. Birds were assumed to occupy a single territory over the non-breeding period (Xenophontos et al. 2017) and this location was estimated as the mean location during the period December to February: this assumption of the fine scale location of the non-breeding site over a few hundred kilometres is trivial in respect to the hypotheses tested here over the scale of several 1000 km.

Wind data

We used zonal (U_{wind} where positive values are eastward) and meridional (V_{wind} where positive values are northward) wind components for analysis, allowing us to describe the winds relative to the overall migration direction. We assumed that negative V_{wind} is supportive during southward autumn migration and positive V_{wind} is supportive during northward spring migration. Regional U_{wind} and V_{wind} components covering the migration periods were downloaded from the ERA5 reanalysis (Copernicus Climate Change Service (C3S) 2017) at four pressure levels (1000, 925, 850 and 700 mbar, corresponding to altitudes of 100, 750, 1500 and 3000 m a.s.l., respectively) encompassing the most likely migration altitudes in the region (Klaassen and Biebach 2000, Bruderer et al. 2018) at 1-hourly intervals with a resolution of 0.25×0.25 degrees. Wind data from all pressure levels were used together in analyses since we do not have flight altitude information to define a specific pressure level during migration, but it is likely that the birds migrated within the analysed range. The median elevation above sea level in the combined migration region is ~500 m, with <0.001% of the area above 3000 m and this is all situated in the non-breeding latitudes.

To analyse the wind conditions during migration we created separate autumn and spring migration regions that extended between the breeding latitude in Cyprus to the most southerly non-breeding latitude. The mean longitude during migration was calculated for each bird for each migration and the maximum and minimum mean longitude including 1 SD (standard deviation) determined the east–west extent of the respective seasonal migration regions. We plotted wind roses displaying the wind vector azimuth and speed (i.e. the direction that the wind is moving towards) for each region during autumn and spring migration for qualitative comparison of general wind patterns between regions and seasons.

We overcame the inherent uncertainty with geolocator data, particularly since our analysis relies primarily on longitude data, by describing the wind experienced by an individual bird during migration at a very low resolution, which although imprecise, still allows for the direct comparison of wind variables between seasons at a large scale. We analysed the U_{wind} and V_{wind} components for each individual spring and autumn migration, with individual wind regions created for each migration. As before, we set the north to south extent based on the breeding and wintering latitude, but the east–west extent was determined by taking the mean longitude during migration $\pm$ 2 SD (i.e. the eastern extent is an individual bird's mean longitude during migration plus 2 SD, and

the western extent is the mean longitude minus 2 SD). We used mean longitude $\pm$ 2 SD at the individual level, rather than 1 SD used for the creating the extents of the general migration regions mentioned above, so that our approach to investigating wind support is conservative. The wind analysis period for each bird's migration was defined as the departure date minus one day to the arrival date plus one day.

We then calculated the mean V_{wind} and U_{wind} wind components for each bird's migration region and period to determine if the wind conditions experienced during migration were supportive. We also calculated the standard deviation of V_{wind} and U_{wind} for each bird's migration region and period to determine how wind variability differed between seasons.

Finally, we compared mean V_{wind} for each bird's autumn and spring migration period in both their east and west migration regions concurrently to determine if the routes they followed in each season provided more support than if they had used the alternative season's route. For this we describe the V_{wind} component relative to the direction of migration and call this 'wind assistance', so that positive values of wind assistance are assumed to be supportive for migration whilst negative values are not, and we then compared the wind assistance for the 'route taken' and 'route not taken' for each bird.

We used linear mixed models to test differences in wind variables between seasons, with year as a random effect in each model.

Results

Observed longitudes in spring all showed a clear eastern detour compared to those in autumn (Supplementary information), so that spring and autumn migrations are consistently on the east and west side of the Red Sea, respectively (Fig. 1). Wind conditions varied between the two different regions used during spring and autumn migration, and this pattern was generally consistent within and between years (Supplementary information). Winds during autumn in the western region are predominantly from the north, providing a tailwind for migration (Supplementary information). These same regions present a consistent headwind in spring, whilst the eastern region has variable wind conditions over the migration periods but with average winds from the south–east in both autumn and spring (Supplementary information).

The routes and timing of the birds were such that winds were supportive on average for both autumn and spring migration. During autumn, mean V_{wind} was (mean $\pm$ 1 SE) -1.43 ± 0.42 m s^{-1}, i.e. from the north, whilst it was 0.89 ± 0.22 m s^{-1} during spring, i.e. from the south (Supplementary information). Mean U_{wind} was similar between seasons ($t_{23}=0.26$, $p=0.80$, marginal $R^2=0.003$), with autumn and spring having mean U_{wind} components of 0.74 ± 0.39 m s^{-1} and 0.85 ± 0.17 m s^{-1} respectively, i.e. from the west (Supplementary information).

Winds during spring migration were more variable than in autumn. Variation in both V_{wind} and U_{wind} experienced by birds during migration was greater in spring than in autumn
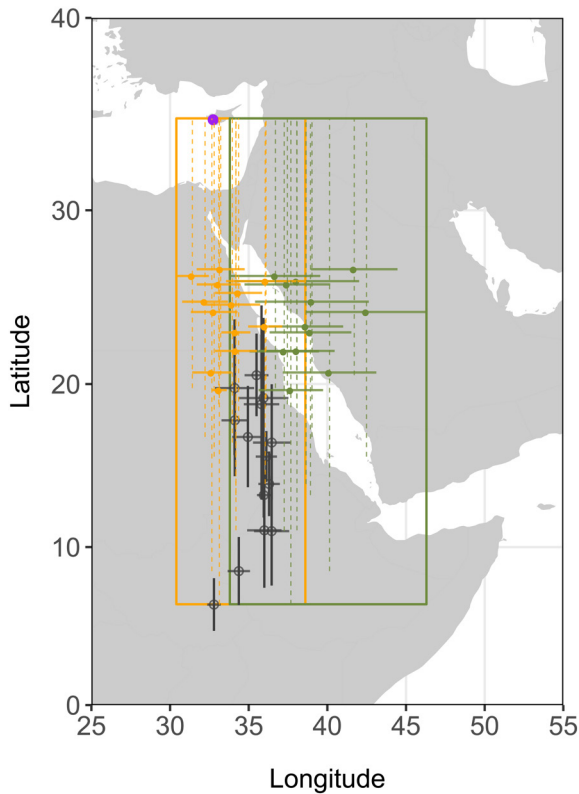
Figure 1. The breeding location of adult Cyprus wheatears (autumn 2014: n = 6; spring 2015: n = 4; autumn 2017: n = 6; spring 2018: n = 7) in Cyprus (purple point) and non-breeding locations for each bird (black points ± 1 SD). The western region used during autumn migration (orange rectangle) and eastern region used during spring migration (green rectangle) with mean longitudes during migration plotted at the mid-point between the breeding and respective non-breeding location for each bird (± 1 SD for longitude [solid line] and dashed line extending from breeding to non-breeding location for each bird to reflect that the data do not include latitude estimates from geolocator data since the migrations occurred near or during the equinox).

(V_{wind}: $t_{22.4} = 5.34$, p < 0.001, marginal $R^2 = 0.53$ and U_{wind}: $t_{22.4} = 8.93$, p < 0.001, marginal $R^2 = 0.76$). The average (mean ± 1SE) standard deviation in V_{wind} experienced by birds during migration in autumn was $4.20 ± 0.12$ m s^{-1} and $5.13 ± 0.12$ m s^{-1} in spring, and standard deviation in U_{wind} in autumn was $3.57 ± 0.17$ m s^{-1} and $5.23 ± 0.09$ m s^{-1} in spring (Supplementary information).

Birds gained significantly greater wind assistance during migration by taking routes in the west region in autumn and the east region in spring compared to if they had taken routes in the alternative region for each migration ($t_{43} = 6.96$, p < 0.001, marginal $R^2 = 0.52$) (Fig. 2).

Discussion

Autumn and spring migration occurred in different regions, each with differing wind patterns. The eastern spring migration detour, crossing the Red Sea, appears to allow access to
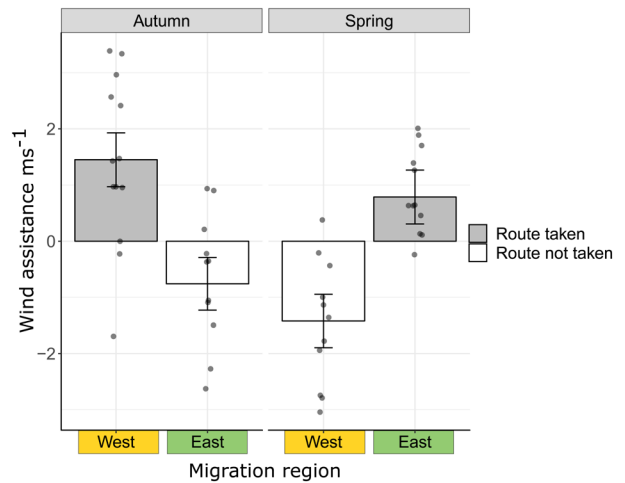

Figure 2. Mean wind assistance (V_{wind} relative to the direction of migration) for adult Cyprus wheatears during autumn and spring migration over the east and west migration regions during 2014–2015 and 2017–2018 (autumn 2014: n = 6; spring 2015: n = 4; autumn 2017: n = 6; spring 2018: n = 7). All birds migrated in the western region during autumn and the eastern region during spring. Error bars show 1SE.

a region of more variable winds that provide greater support for migration than if birds returned to the breeding grounds following the same direct route as in autumn.

Our approach is necessarily coarse in scale but appropriate because it reflects the limitations of only using longitude data, not having flight altitude data, as well as the error associated with geolocator data. That we found a significant pattern in spite of these limitations underlines that the differences between spring and autumn migrations and their associations with regional wind conditions are strong.

The anti-clockwise loop migration around the Red Sea has been observed in Eleonora's falcon *Falco eleonorae* and the seasonal difference in route over this part of their migration between Cyprus and Madagascar was also linked to prevailing wind conditions (Hadjikyriakou et al. 2020). Common swifts *Apus apus* migrate directly over the Sahara during autumn but take alternative routes in spring to gain wind assistance, where the eastern most route during spring migration crosses the Arabian Peninsula (Akesson et al. 2016) similarly to the Cyprus wheatear. The spring migration of red-backed shrike *Lanius collurio* also follows an eastern detour through the Arabian Peninsula that is thought to optimise wind assistance (Tøttrup et al. 2017). Similar patterns have also been observed in other flyways. Tree swallows *Tachycineta bicolor* for example, cross the Gulf of Mexico directly in autumn but follow a detoured overland route in spring and this is also linked to prevailing wind conditions (Bradley et al. 2014). These examples all involve crossing barriers, such as the Sahara, where wind assistance appears to play an important role in the route taken and can also impact survival (Loonstra et al. 2019). Barrier crossings and regional wind patterns then, may explain many of the reported loop migrations.

The differing wind patterns described in the two migration regions are consistent between the two years of the study and

with other studies that describe air circulation in the region (Erni et al. 2005, Athar and Ammar 2016, Patlakas et al. 2019). Other loop-migrations in the Afro-Palearctic flyways may also be driven by these particular (Finch et al. 2015, Briedis et al. 2018b) or similar (Norevik et al. 2019) wind patterns, and seasonally predictable wind patterns (La Sorte et al. 2014) along with the distribution of suitable stopover habitat (Stach et al. 2016) may explain observed seasonal differences in migration routes more generally.

The spring detour may also increase feeding opportunities that are unavailable whilst crossing the Sahara directly in a headwind, and it is also possible that Cyprus wheatears use mainland staging areas with reliable food resources prior to arriving on the breeding grounds in Cyprus, allowing them to fine tune their arrival time (Tøttrup et al. 2010). This may, however, not be crucial to our study population because Cyprus wheatears at Troodos often arrive when there is extensive snow cover and can wait up to one month before the onset of breeding, although the species may be more strongly time constrained for arrival at the breeding ground where it breeds at lower altitudes in Cyprus. The relatively short migration distance between the breeding and nonbreeding ground (ca 3000 km) (Xenophontos et al. 2017) in comparison to other trans-Saharan migrants may also allow for greater flexibility in the modification of departure timing and final breeding ground arrival.

Although we provide circumstantial evidence that Cyprus wheatears shape the route of their migration according wind conditions, many other variables, that could not be considered in this study because of the low resolution of locations during migration, such as the availability of stop-over habitat (Stach et al. 2016), may also influence these migration routes. These other drivers of seasonal differences in migration strategy may be more or less important than wind in determining how a species may respond to environmental change, but it seems likely that wind conditions must be generally important if continental scale detours arise in correlation with them.

The observed differences between autumn and spring migration routes of Cyprus wheatears suggest some scope for adjustment to future changes in wind conditions. Loop migrations related to prevailing winds are common (La Sorte et al. 2014) suggesting that many long-distance migrants may also be well adapted to cope with changes in wind conditions (Loonstra et al. 2019) that may be either positive or negative depending on the region or season (La Sorte et al. 2019). The mechanisms that might underlie capacity to adapt to changing wind conditions though, e.g. modifying routes at the individual level (Teitelbaum et al. 2016) or through generational change (Cresswell 2014, Gill et al. 2019), require further investigation, particularly in passerines where high resolution data and repeat tracking of individuals are lacking.

Transparent Peer Review

The peer review history for this article is available at https://publons.com/publon/10.1111/jav.02466

Data deposition

Data will be available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3tx95x6dm> (Patchett and Cresswell 2020).

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