Migration of red-backed shrikes from the Iberian Peninsula: optimal or sub-optimal detour?

Anders P. Tøttrup, Lykke Pedersen, Alejandro Onrubia, Raymond H. G. Klaassen and Kasper Thorup

A. P. Tøttrup (aptottrup@snm.ku.dk), L. Pedersen and K. Thorup, Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, Univ. of Copenhagen, Denmark. – A. Onrubia, Fundación Migres, CIMA (International Bird Migration Center), Tarifa, Spain. – R. H. G. Klaassen, Dutch Montagu's Harrier Foundation, Scheemda, the Netherlands, and Conservation Ecology Group, Groningen Inst. for Evolutionary Life Sciences, Univ. of Groningen, Groningen, the Netherlands.

The current Northern Hemisphere migration systems are believed to have arisen since the last glaciation. In many cases, birds do not migrate strait from breeding to non-breeding areas but fly via a detour. All western European populations of red-backed shrikes *Lanius collurio* are assumed to reach their southern African wintering grounds detouring via southeast Europe. Based on theoretical considerations under an optimality framework this detour is apparently optimal. Here, we use individual geolocator data on red-backed shrikes breeding in Spain to show that these birds do indeed detour via southeast Europe en route to southern Africa where they join other European populations of red-backed shrikes and return via a similar route in spring. Disregarding potential wind assistance, the routes taken for the tracked birds in autumn were not optimal compared to crossing the barrier directly. For spring migration the situation was quite different with the detour apparently being optimal. However, when considering potential wind assistance estimated total air distances during autumn migration were overall similar and the barrier crossing shorter along the observed routes. We conclude that considering the potential benefit of wind assistance makes the route via southeast Europe likely to be less risky in autumn. However, it cannot be ruled out that other factors, such as following a historical colonisation route could still be important.

Migratory birds are capable of flying long distances across barriers without possibilities of stopping over (Gill et al. 2009). Even for small songbirds, long-distance flights across barriers have been reported (Bairlein et al. 2012, Deluca et al. 2015). However, there are many examples of migratory bird species following alternative routes that differ from the direct path between departure and destination even though they are energetically capable of making long distance flights (Alerstam 2001). Based on ring-recoveries and observations, all populations of red-backed shrikes *Lanius collurio* from Europe are believed to initiate autumn migration with a first leg of migration to southeast Europe, and then follow the same migration corridor southwards to the Sahel (Korner-Nievergelt et al. 2012).

According to migration theory, migration can be optimized by minimizing a simple currency such as energy cost of transport, time or mortality, or a combination, as for example total energy cost of migration (Hedenström and Alerstam 1997). If considering migratory birds to follow routes that minimize overall fuel transportation cost, birds will save energy by short flights with low fuel loads compared to long flights with large fuel loads. Therefore, birds are expected to accept a certain detour distance where shorter flight steps can be applied and avoid ecological barriers where food supply is low and more fuel is needed for

successful completion of their migration (Alerstam 1979). Thus, in terms of energetics, the cost of transporting heavy fuel loads across a long barrier may be overcome by travelling along a detour with the possibility of making shorter stopovers requiring smaller fuel loads.

The adaptive value of making a detour may depend on multiple factors related to migratory travelling (avoiding hazards) as well as stopping over (associated with a suitable environment) (Alerstam 2001, 2011, Hahn et al. 2014). Factors favouring a route include potential wind assistance (Erni et al. 2005, Vansteelant et al. 2016), habitat and food availability (Alves et al. 2012, Thorup et al. 2017) whereas potential hazards include side-wind drift, high probability of head winds, high predation risk (Klaassen et al. 2006, Ydenberg et al. 2007, Bauer et al. 2010, Gill et al. 2009), and sea and desert crossing (Biebach et al. 1986, Barboutis et al. 2011). Alternatively, detours could be constrained by historical patterns of dispersal and colonization events (Irwin and Irwin 2003).

To investigate whether detours from the direct path would be optimal in terms of energy cost of transport, Alerstam (2001) developed a theoretical framework based on flight mechanics (Pennycuick 2008) and optimality theory (Alerstam and Lindström 1990). Predictions were based on models derived from range equations on flapping

flight (Alerstam and Hedenström 1998) and several detours were evaluated, including a detour to north-eastern Sahel via Greece for red-backed shrikes breeding in southern France. Assuming that the red-backed shrikes were migrating in short hops before fattening up for the barrier crossing over the Mediterranean and Sahara, the extra detour was found to be advantageous over a direct crossing regarding travel costs (Alerstam 2001). Nevertheless, a proper evaluation of this detour requires detailed knowledge of the individual spatiotemporal schedules followed when detouring and crossing. Erni et al. (2005) showed winds to be equally important for optimal detours.

Continuous advances in tracking technology now enable us to track individuals, allowing us to test theoretical predictions using the framework developed by Alerstam (2001) on observed tracks. Here, we use empirical data collected by direct tracking of red-backed shrikes using archival light-level loggers (geolocators) from a breeding site in north-western Spain to evaluate whether the original predictions hold when considering individual routes compared to a direct route toward staging sites in the Sahel and a southern detour with direct crossing of the Sahara from breeding grounds. In addition, we evaluate the potential effects of wind assistance along these routes taking individual timing of migration into account.

Methods

Geolocator deployment and recovery

We tracked individual red-backed shrikes by use of archival light-level loggers (geolocators: Mk10s (8 mm stalk; weight 1.1 g) in 2011 and Mk10 (without stalk; weight 1.1 g) in 2012 developed by the British Antarctic Survey (BAS) and Intigeo P65 (without stalk; 0.75 g) in 2013 developed by Migrate Technology) from a breeding site in Leon, Spain (42.65°N, −5.51°E) during three consecutive years (2011–2013). At logger attachment the birds weighed 25–37 g. Thus, the logger represented a maximum of 4.4% of the body mass. Loggers were attached using a leg-loop backpack harness (Naef-Daenzer 2007). A total of 60 geolocators were deployed (20 each year) and in the following years 11 birds were relocated in the area. Two birds where not possible to recapture, one bird had lost the geolocator and one bird returned with a logger without data. One of the seven individuals returned with a geolocator containing data from two consecutive full annual cycles and one individual were trapped twice in two consecutive years. Thus, we obtained useful tracking data from six individuals with eight tracks. The return rate of 18% is similar to what has been found in other studies (17%) on this species (Tøttrup et al. 2012a, b).

Light data analyses

Data were adjusted for clock drift and false twilights caused by shading events were removed using the R package BAStag (Wotherspoon et al. 2013). Here, all twilight events are compared to the twilight events of the preceeding and following day, allowing for visual inspection and removal of twilight events that show non-random changes in shading (false twilights). We used a threshold of 2 for BAS geolocators and 0.3 on log-transformed data for Intigeo geolocators to define twilight times. In between 6–56 twilights were removed for each individual (Supplementary material Appendix 1, Table A1). Occurrence of false twilights seemed to be randomly distributed throughout the annual cycle for all individuals. Positions were generated from light data using the R package GeoLight (Lisovski and Hahn 2012). Latitudinal data for up to three weeks on both sides of equinox was excluded (tolerance: 0.10–0.16) (Fudickar et al. 2012). For calibrating the data, we followed the Hill–Ekstrom calibration procedure (Hill and Braun 2001, Ekstrom 2004) described in detail in Tøttrup et al. 2012b.

Route estimation

We defined 'staging site' as areas where birds interrupted migration for more than five days, although birds could have moved short distances within a given area. Departure and arrival dates were determined from longitudinal and latitudinal positions; during equinox periods only from longitude. The length of the migration detour by tracked individuals was calculated as the sum of distances in between estimated individual mean positions of consecutive staging sites. For autumn migration the detour consisted of the following two stages: (A1) breeding area to south-eastern Europe and (A2) south-eastern Europe to the Sahel region in north-eastern Africa, where the barrier distance was defined as the length of the second of these stages. Likewise for spring migration, sequences were divided into two stages: (S1) north-eastern Africa to the point where birds change direction at the Arabian Peninsula (defined as the north-eastern most point while the bird was at the Arabian Peninsula), and (S2) from the change in direction at the Arabian Peninsula to the breeding area. To estimate the end of the barrier we defined a longitudinal border line (36.5°E) when birds cross over from the Arabian Peninsula into Turkey. We then used the longitude of the individual first position after the crossing and a latitude of 36.5°N for all individuals. The length of the barrier was thus defined as the distance from the staging site in north-eastern Africa up to this point following the route with a change in direction at the Arabian Peninsula (Fig. 1C). For one individual (id: 59) it was not possible to estimate a spring migration route over the Arabian Peninsula due to poor data quality (Supplementary material Appendix 1, Fig. A2). The direct route was measured as the length between the breeding area and the individual mean positions of the staging area in the Sahel region on autumn migration and north-eastern Africa on spring migration, respectively. The barrier was estimated as the distance from the coastline of Spain to and from the staging site in Sahel and north-eastern Africa, respectively.

As alternative routes, we defined for autumn migration a western detour going straight south from the breeding area into the Sahel region in western Africa (point location: 15.0°N, −5.51°E), corresponding to the birds having crossed the Sahara desert in mid-August. Likewise, for spring migration we defined a western detour with a stopover in western Africa (point location: 11.5°N, −5.51°E),
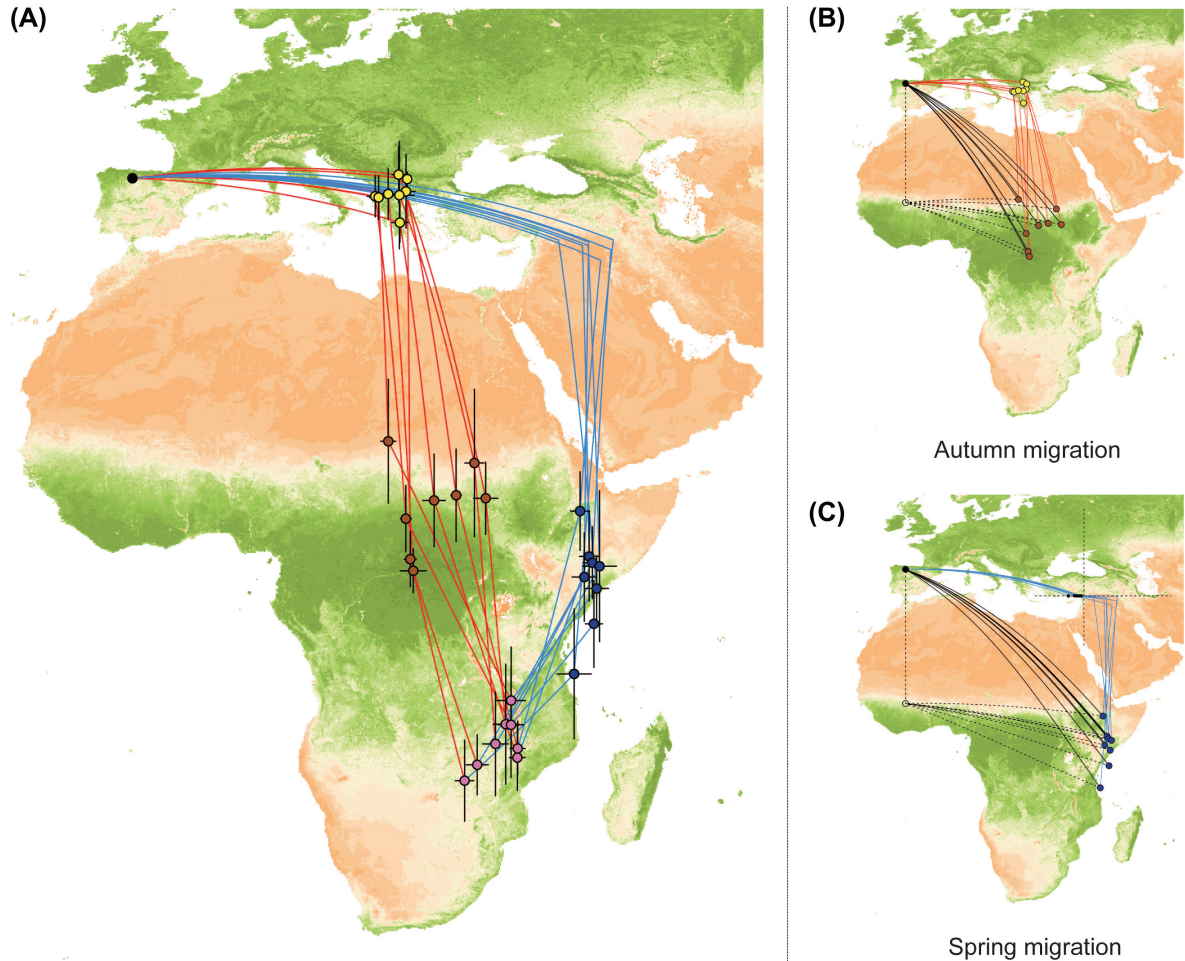
Figure 1. (A) Main stopover sites (± standard deviation of longitudinal and latitudinal variation in positions) in south-eastern Europe (autumn: yellow), north-eastern Africa (autumn: brown), non-breeding areas in southern Africa (pink) and north-eastern Africa (spring: dark blue) of eight tracks from six individual red-backed shrikes *Lanius collurio* from their breeding sites in north-eastern Spain. Red and blue tracks indicate autumn and spring migration routes, respectively. Temporal details and individual migration positions are presented in the Supplementary material Appendix 1, Table A1 and Fig. A1. (B, C) Direct route (black lines), tracked (red/blue lines for autumn and spring, respectively) and potential detour (dashed lines). Open black circles show a possible stopover site along the potential detour across western Africa. Dashed cross represent the definition of the end of the barrier crossing on spring migration and small black circles the position at which individuals are assumed to have crossed the barrier. Background maps represent MODIS MOD13C1 16-d normalized difference vegetation index (NDVI) values at 500 m resolution in mid-August 2000–2015 (autumn, B), mid-May 2000–2015 (spring, C) and average values across seasons 2000–2015 (A), respectively.

corresponding to the birds making a stop just before reaching the Sahara desert in mid-May. Barrier distance was estimated from the southernmost point of Spain. All distances were calculated as great circle distances on an ellipsoid between geographical point locations (R package: Geosphere (Hijmans 2015), function: distVincentyEllipsoid).

Wind estimation

To estimate the effect of wind on the choice of a detour we linearly interpolated dates and corresponding positions along the great circle line between all legs of migration (R package: Geosphere (Hijmans 2015), function: gcIntermediate with 50 intermediate points between every migration legs). For one individual (id: 38) where breeding area arrival was not available due to battery failure we assumed a mean arrival date at the breeding grounds. Likewise, for the direct route

and the western detour we used mean departure and arrival between start and endpoint.

For the staging site along the western detour we assumed a mean arrival and departure date from the staging site in southern Europe in autumn and spring, respectively.

For every location wind data were obtained from the NCEP/NCAR Reanalysis project, as provided by the NOAA/OAR/ESRL PSD, Boulder, CO, USA (< www.cdc.noaa.gov >), using the NCEP.interp function in the RNCEP R package (Kemp et al. 2012a). These data consist of west–east (u-winds) and south–north (v-winds) wind components, which were combined into single wind vectors (i.e. direction and strength of the wind). Data were extracted for two pressure levels, 850 and 700 hPa, which corresponds to altitudes of about 1500 and 3000 m a.s.l., respectively. These altitudes were selected because the largest volume of passerine migration occurs at these heights (Schmaljohann

et al. 2009). The two wind vectors obtained per location for the two altitudes were averaged. Subsequently, we calculated, for every wind vector, the tailwind components, with the direction of the migration segment as the reference direction (following Kemp et al. 2012b). These tailwinds were used to calculate, per migration segment, the air distance (i.e. the distance the bird travelled with reference to the surrounding air, i.e. taking the tailwind into account), which were compared to the ground distances (i.e. distance travelled with reference to the ground).

When comparing the detour flight with the potential direct migration route, we assume that individuals migrate by short flight steps and carrying small fuel loads in non-barrier areas, whilst longer staging periods to restore heavy fuel loads are restricted to areas just in front of barriers (Alerstam 2001). To validate this assumption we examined plots of longitudinal positions during autumn migration (stage A1) (Supplementary material Appendix 1, Fig. A1). However, for spring migration (non-breeding area in southern Africa to the staging site in north-eastern Africa) the movement was primarily latitudinal and partly shadowed by the equinox period.

Data available from Movebank Data Repository: < doi: 10.5441/001/1.32m2335q> (Tøttrup et al. 2016).

Results

Spatio-temporal migration pattern

The full annual cycle migration of Spanish red-backed shrikes consisted of four main staging sites: south-eastern Europe (autumn, mean duration: 13 d ± SD = 4.3), Sahelian north-eastern Africa (autumn, mean: 46 d ± 7.4) southern Africa (austral summer, mean 129 d ± 8.8) and north-eastern Africa (spring, mean: 9 d ± 2.5) (Fig. 1A, Supplementary material Appendix 1, Fig. A2).

Individuals initiated autumn migration in early August (mean date: 7 August, range of dates: 1 August–23 August)

and arrived at the southern African non-breeding site in November/December (mean: 22 November, range: 10 November–7 December). Timing of arrival and departure to and from the in-between staging sites were as follows: southern Europe (mean arrival: 19 August, range: 13 August–7 September; mean departure: 2 September, range: 24 August–22 September) and Sahelian north-eastern Africa (mean arrival: 10 September, range: 29 August–30 September, mean departure: 26 October range: 18 October–10 November).

Spring migration was initiated from southern Africa in March/April (mean date: 31 March, range: 20 March–9 April) and all individuals had at least one stop in north-eastern Africa where they arrived in April (mean date: 17 April, range: 5 April–25 April) and departed in April/May (mean date: 26 April, range: 17 April–4 May) before crossing the Arabian Peninsula and returning to the breeding grounds in May/June (mean date: 27 May, range: 20 May–7 June) (Supplementary material Appendix 1, Table A1).

Detour

Our tracking data indicate direct crossing of the desert areas and we find no indications of staging sites between the breeding area and south-eastern Europe prior to the barrier crossing during autumn migration (Supplementary material Appendix 1, Fig. A1). Because of Equinox this could not be evaluated for the migration between southern Africa and north-eastern Africa during spring migration (Supplementary material Appendix 1, Fig. A2).

Extracting the length of the relevant legs from our direct tracking data and inserting these into the theoretical models developed by Alerstam (2001), we find that the detoured flight (Fig. 1B) on autumn migration is energetically sub-optimal compared to the direct flight from the breeding area towards a main staging site in north-eastern Africa for all tracked individuals (Fig. 2). Similarly, the alternative route via western Africa seemed to be sub-optimal compared to
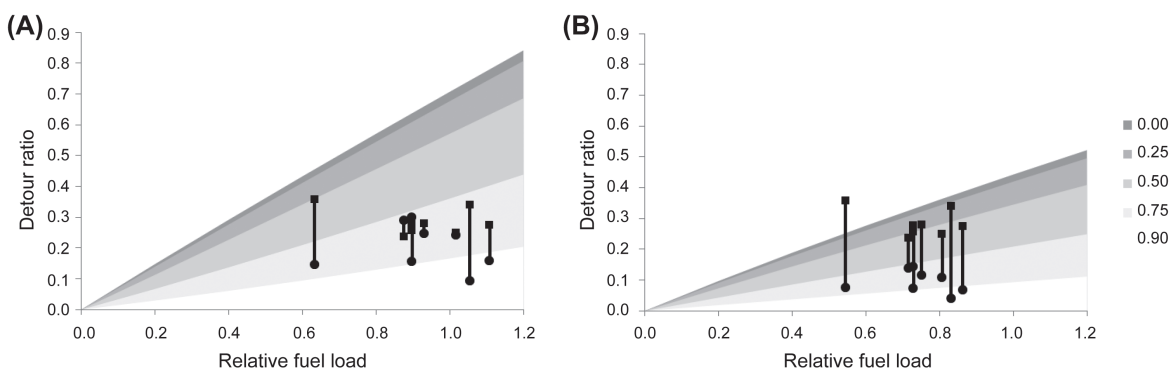

Figure 2. Maximum detour ratios (the extra distance along detour relative to barrier distance) as a function of relative fuel load required to cross the barrier in a single flight during the autumn (Fig. 1) based on two flight range equations assuming that fuel load increases both induced and parasite drag (A) and fuel loads only increases induced drag (B) (Pennycuick 1975) with the true relationship presumably being intermediate between these two equations (Alerstam and Hedenström 1998). Grey shading indicates different fractions of the barrier included in the detour assuming that the remaining part of the detour is completed by short flights without fuel transport costs. (Figure is modified from Fig. 6 in Alerstam 2001.) Based on our direct tracking of six individual red-backed shrikes (eight tracks in total), squares gives the detour ratios predicted from theory in relation to calculated relative fuel load. The circles are the theoretically predicted detour ratio given the estimated relative fat loads. The theoretically predicted maximum detour is smaller than the observed detour except in one case (modified from Alerstam 2001). The maximum detour ratios for the alternative western routes (Fig. 1A–C) related to the direct route is presented in Supplementary material Appendix 1, Fig. A3.

the direct flight. For spring migration (Fig. 1C), the detour was energetically favourable compared to the direct flight for all tracked individuals as was the potential alternative route across western Africa. However, the required fuel loads became unrealistically high (> 1.3) for all tracks following the modeling approach: both the observed tracked detour and western alternative detour compared to the direct route.

Potential wind assistance resulted in overall shorter air distances than ground distances for autumn migration (Fig. 3). Wind assistance was on average greater for the observed, detoured route than for the direct route, resulting in similar total estimated air distances (Fig. 3). In fact, for four of eight tracks, estimated air distances were shorter along the observed route (Supplementary material Appendix 1, Fig. A4). In spring, the air distances were longer than ground distances for the direct route (Fig. 3, Supplementary material Appendix 1, Fig. A4B).

Discussion

Our trackings confirm the suggested autumn route via Greece for western European populations of red-backed shrikes based on ring recoveries (Korner-Nievergelt et al. 2012). From there, the route and timing to the wintering grounds in southern Africa with a stopover in north-east Sahel are similar to north European populations (Tøttrup et al. 2012b). Our trackings also confirm that the eastward migration is in short almost daily flights, whereas from the southeast Europe, the birds cross the barrier relatively fast (Supplementary material Appendix 1, Fig. A1 and Table A1, see also Bäckman et al. 2016). The spring route northwards from the wintering grounds via the Horn of Africa is also similar both spatially and temporally until the birds turn abruptly westwards over the Arabian Peninsula and travel along the north Mediterranean.

Based on our evaluation of the energy cost of transport of this migration, the autumn detour appears sub-optimal. This finding is in contrast to the original evaluation in

Alerstam (2001). The most important reason for our contrasting result is that 1) our birds start in north-eastern Spain instead of southern France adding approximately 1000 km to the detour (slightly less to the direct crossing) and 2) the stopover in south-eastern Europe is located further north than assumed by Alerstam, resulting in a considerably larger proportion of the barrier crossing being included in the detour (Alerstam 2001). In fact, for several of the tracked birds, the actual barrier crossing was even slightly longer than the direct flight.

For spring migration the situation was quite different with the detour apparently being optimal. The theoretical evaluation of the observed tracks indicates energetically sub-optimal routes taken similar to the situation in autumn.

Wind is important for energetics of the travelled ground distances potentially significantly altering air distances (Alerstam 1979). Our estimates of winds along the route options in autumn show that significant tail wind assistance is to be expected along the observed, detoured route with air distances being similar for the direct crossing and detoured routes. Thus, considering wind assistance both routes appear equally favourable. The overall shorter barrier crossing for the detoured route in combination with at least some suitable foraging habitat during the crossing (Hahn et al. 2014) potentially minimise hazards in the long run (though the barrier crossing route does appear to be west of the Nile where only little such habitat is available). It seems that the detoured migration in the shrikes is in fact favourable compared to the direct crossing. It is possible that retracing a historical colonisation route guided by an innate migration programme could still have given rise to this migration route, and our framework does not allow for comparing all potential migration routes.

Previous studies have indicated little variation between years in migration timing, routes and stop-over sites (Tøttrup et al. 2012b), whereas others indicate that migration timing and route are relatively flexible (Sutherland 1998, Alerstam 2001). Potentially, the many detoured migration routes observed could have different underlying causes with some being optimal given wind assistance and availability of foraging habitat whereas others are constrained by the migration programme. Understanding these differences requires improved information of the migration programme and how it develops with experience in migrants (Sergio et al. 2014). Hopefully, the ability to track more species will enable the evaluation of more detours and thus a better understanding of how the routes have evolved.
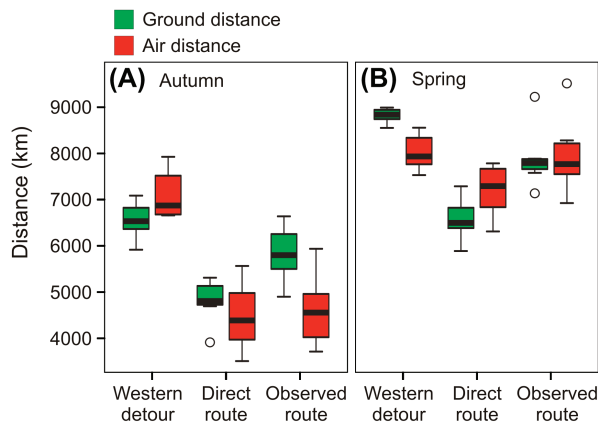

Figure 3. Mean ground and air distances for autumn and spring migration along the three different routes (Fig 1). All distances were calculated as great circle distances on an ellipsoid between geographical point locations (R package: Geosphere (Hijmans 2015), function: distVincentyEllipsoid). See details in the Methods sections.

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