

Spatiotemporal group dynamics in a long-distance migratory bird

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Summary

Thousands of species migrate [1]. Though we have some understanding of where and when they travel, we still have very little insight into who migrates with whom and for how long. Group formation is pivotal in allowing individuals to interact, transfer information and adapt to changing conditions [2]. Yet it is remarkably difficult to infer group membership in migrating animals without being able to directly observe them. Here, we use novel lightweight atmospheric pressure loggers to monitor group dynamics in a small migratory bird, the European bee-eater (*Merops apiaster*). We present the first evidence of a migratory bird flying together with non-kin of different ages and sexes at all stages of the life cycle. In fact, 49% stay together throughout the annual cycle, never separating longer than 5 days at a time despite the ~14,000 km journey. Of those that separated for longer, 89% reunited within less than a month with individuals they had previously spent time with, having flown up to 5,000 km apart. These birds were not only using the same non-breeding sites but displayed coordinated foraging behaviours – these are unlikely to result from chance encounters in response to the same environmental conditions alone. Better understanding of migratory group dynamics, using the presented methods, could help improve our understanding of collective decision-making during large scale movements.

Results

From zebras [3] to monarch butterflies [4], migratory species undertake some of the most extreme feats of endurance known in the animal kingdom. With the advent of novel tracking technologies, we are gradually completing the picture of where and when they travel [5]. However, without being able to directly observe migration [e.g. 2], we have very little knowledge of who might migrate with whom.

Migratory species are notable for their propensity to aggregate in large numbers. The stability of migratory groups over time can be important in determining survival [6], navigational accuracy [7], migratory speed [8], transfer of information [7] and new migratory behaviours [2]. However, migrating with others is not without risk, as it can increase both disease prevalence [9] and resource competition [10]. Group size typically fluctuates over time and space, with individuals coming together and separating [11; hereafter termed “fission-fusion dynamics”] as they trade-off the different benefits and costs of cooperation [11,12]. Indeed, resource patches are distant, seasonal and often unpredictable. One slow individual could, for instance, force the entire group to slow down and miss peaks in resource availability, creating conflict [11]. Groups can therefore either compromise to remain together, or split into sub-groups, for example of different migratory speeds.

Fission-fusion can occur without individuals being able to “recognise” each other *per se* [11]. The same individuals could encounter each other again and again at the same site as a result of migratory connectivity, simply because it is the only one available to them at a particular period [13–15]. Under such circumstances, resource bottlenecks are likely driving group fusion, not social relationships [14]. On the other hand, where resources occur broadly over a large area, animals must coordinate decisions to fuse into a long-term group, especially if they regularly fissure and must find each other again [13,16]. Only species with high social cognition, such as elephants [17], dolphins [18] and bats [19] have been found to form long-term social bonds by coordinating decisions, despite separations imposed by migration. In birds, long-term social bonds despite fission-fusion dynamics have been observed between non-migratory non-kin [20,21], migratory kin [22], or migratory bonded-pairs [23]. Long-term social bonds, despite fission-fusion dynamics are poorly understood in non-kin migratory birds.

Here, we use novel lightweight (~1.4g) multi-sensor loggers to track the spatiotemporal pattern of group cohesion between 29 European bee-eaters (Figure S1A; *Merops apiaster*) over the annual cycle. Indeed, European bee-eater are gregarious. They can breed cooperatively, making complex decisions on whether to help another breeding pair, which pair to help and how much [24]. The species also forages socially [25], and can cooperate with other bee-eater species to mob predators, preen and forage [26] In the non-breeding grounds, they form vocal flocks of 8 individuals (on average with a range of 5-40 individuals based on e-bird data from the non-breeding grounds [27]), 8-39 during stopover [28] and of 30-100 during migration [29,30]. However, what is less well established is how gregariousness might change over time. More specifically, we aim to determine (i) whether birds from the same colony have similar migratory routes, (ii) whether they remain together during migration, (iii) what the stability and (iv) composition of these groups might be.

We used novel multi-sensor loggers to measure both light for geolocation, and ambient air pressure for altitudinal changes during the annual cycle (2015 to 2016 and 2016 to 2017). To confirm potential groups suggested by geolocation overlap (Figures 1 vs S1B), we applied a hidden Markov model

(HMM) to ambient air pressure measurements and identified periods of synchronisation in altitudinal changes between birds (Figures 2 and S2). Indeed, altitudinal changes can easily be identified from the pressure measurements: background variations in pressure driven by weather are less than 2 hPa per hour, while those caused by flight range from 2-205 hPa per hour (equivalent to a change in altitude of 16.89-1934.97m assuming a starting pressure of 1000 hPa at 15°C; Figures 2 and S2E-F). We assume that if these highly dynamic altitudinal changes are synchronous, then the decision to fly/not fly, to go up/down, how high/low is coordinated between individuals. Thus, if some individuals made the same decision at the same time repeatedly, especially over weeks or months, the decision must have been shared between individuals flying within the same flock.

To test the method, we then compared birds within the same breeding colony (Figure 3A) and found that even birds that were nesting within 500m from each were not always classified as having similar pressure signatures (Figures 3A and 3E). Thus, the observed patterns are likely driven by behaviour, not overestimated due to geographic proximity or weather fronts (Figure S2E and F).

Even within a relatively small sample size of 29 tagged individuals recaptured between 2016 and 2017, 89% formed long-term groups with one or more other tagged individuals outside the breeding grounds (Figures 3, 4, S3 and S4). Many groups formed in the breeding grounds prior to migration (Figures 3A and 4) with none of the recaptured individuals having bred together before (Table S1). In total, we identified one group of five individuals (group 1), one group of four (group 5), and six groups of two (groups 2, 3, 4, 6, 7 and 8; Figures 1, 3 and 4). The group of four (group 5 i.e. 19% of grouped birds) persisted throughout the annual cycle, covering 14,000 km together (Figures 1, 3 and 4). HMMs never classified these individuals as having separated during migration (Figure 4). Only, during the non-breeding residency period did we observe individuals breaking into subgroups for short periods of no longer than 5 days (e.g. 2-6th November 2016; Figure S3K).

For two groups (1 and 6 i.e. 33% of grouped birds), fission occurred during southward migration for 5 and 4 days respectively (Figures S4A, B, M and N). Group 1 fissured into two sub-groups while crossing France, while group 6 fissured while crossing Algeria (Figures S4A and M). Both groups fused again to remain stable during the rest of migration, crossing the Sahara and spending their non-breeding residency repeatedly coming together and separating (Figures 4A and F). Group 1 occasionally formed subgroups for a maximum of 9 days before fusing again (Figure S3G). Group 6 only separated for 1 or 2 days at a time (Figure S3L). Group 1 then migrated north to the breeding grounds as a stable group, without separating (Figures 3 and 4). For group 6, fission-fusion dynamics remain unknown because the pressure logger on individual OF failed during the non-breeding season (Table S1).

All other groups (2, 3, 4, 7 and 8 i.e. 48% of grouped birds) started migration from their breeding grounds to their non-breeding grounds together (Figure 4). Of these bonded birds, 80% (groups 2, 3, 4

and 7) parted from their flight partner while crossing the Sahara (Figures 4 and S4). Of these separated birds, 80% (groups 2, 3 and 4) then came back together, having migrated up to 5,000 km over one month separately, in their non-breeding grounds spread across Cameroon, Equatorial Guinea, Gabon, Congo, Democratic Republic of Congo and Angola (Figures 3, 4, S3 and S4D, E and I). Pressure loggers failed on both individuals in group 4, however, groups 2 and 3 then started migrating north to the breeding grounds together, but separated after crossing the Sahara, only meeting again in the breeding colony (Figures 4 and S4H and L).

Also, 17% of birds did not migrate with any tagged birds, but repeatedly joined a group in the non-breeding grounds (Figures 3C and S3A-F; UT and TV joined TY-UK, AA sometimes joined TY-UK and sometimes TZ-UG, and SH and RZ joined BL-RH-TQ-TW-UO). In fact, two groups (3 and 4) occasionally foraged together in the non-breeding grounds, particularly with UG foraging more often with AA than its migratory partner TZ (Figures 3 and S3F), and AA in turn foraging with TY-UK-UT (Figures 3C, S3B and S3E). Most of these birds were already classed as having foraged together in the breeding grounds prior to migration (Figure 3).

Two breeding pairs formed after migration together: TQ-UO from group 1 and OO-OI from group 5 (Table S1). In fact, UO switched colonies from 2016 to 2017 to breed with TQ, though both birds already foraged together in the breeding grounds in 2016, as did OO and OI in 2015 (Table S1 and Figure 3). Neither pair bred together in the year before they were tagged, suggesting that these migratory groups formed independently from pair formation the previous year (Table S1). In total, 8 birds switched breeding colonies, 5 of which moved to the colony of their travel companion (i.e. UO-TW to the breeding colony of BL-TQ-RH, SJ to SO, TY to UK, and TZ to UG; Table S1 and Figure 3A vs 3E). All in all, group formation was not consistent with age or sex, and no birds were ever ringed or tagged within the same burrow before this study, indicating they were not likely kin or previously bonded pairs (Table S1). Indeed, roughly 80% of the juveniles from these colonies have been ringed since 2003 and over 95% since 2007 [31].

Discussion

Without physically following birds with an ultralight aircraft [e.g. 7], it has previously been impossible to monitor spatiotemporal group dynamics in small migrating birds. Here, we show how novel lightweight multi-sensor loggers can be used to better understand who migrates with whom at all stages of the annual cycle. Indeed, our analyses provide strong evidence for long-term group formation in a small migratory bird both during migration and in the non-breeding grounds, between non-kin of mixed age and sex. Though our results do not exclude the possibility of tagged birds forming groups with non-tagged kin, our sample size only included non-kin. This is particularly rare between non-kin, as there is no direct genetic benefit to be gained from remaining together over long

periods. In fact, this is some of the first evidence of migratory birds remaining in long-term non-kin groups throughout all stages of the annual cycle. Despite evidence of waterbirds migrating in non-kin groups, most research indicates that these groups still separate into family or same sex and age sub-groups in the non-breeding grounds, most frequently unpaired juvenile [2,7,32,33].

During migration, theory suggests that stable groups may arise as a result of environmental bottlenecks or social interactions [34], with the importance of sociality increasing with decreasing group size [34,35]. Given that hundreds of bee-eaters migrate simultaneously in flocks of 5-39 individuals [27–30] and that they encounter difficult flight conditions [36], we expected high fission-fusion [11,34]. Indeed, soar-gliding requires birds to identify suitable thermal updrafts, adjust their speed to navigate within the updraft and then find the right moment to leave with enough momentum to get to the next updraft [37]. Older individuals are therefore better at navigating this challenge than younger individuals [37] and species such as storks rarely remain together long-term despite short-term coordination [38,39]. It is therefore surprising that all birds remained together during these periods of rapid altitudinal changes for a minimum of 3 weeks, and 45% during the entire migratory period, hinting at some social aspects to group stability [34]. Though our data cannot directly measure sociability, it is well documented in the species at different stages of the annual cycle [24–26,36],

Surprisingly, of the separated migratory groups 89% reformed again in the Congo Basin [40], an area of roughly 4 million km² with individuals they had previously interacted with in the breeding grounds or on migration (Figures 3 and 4). To some degree, non-breeding range can be genetically driven [41], forcing birds into the same region where they form groups due to proximity. For this population however, the non-breeding ranges are not necessarily overlapping (Figure S1C-J), and sparsely spread out over thousands of kilometres between Gabon and Angola [40]. Given (i) the lack of resource bottlenecks in the region which might force all birds into the same tree or waterhole [11,34], (ii) the fact that non-breeding flocks are relatively small (average size of 8 [27]) [35], and (iii) that separated individuals primarily reunited with individuals they had previously spent time with – suggests these reunions may not have occurred by chance. Indeed, the only individual which was tagged over two years (OO in 2016 and TO in 2017) returned to the same breeding site both years, suggesting that individuals could be returning to sites that they had used with other flock members in the past. However, the mechanisms by which separated individuals reunited despite long separations remains to be elucidated.

The benefits of cooperation, both in the non-breeding grounds and during migration, may explain the need to reach consensus decisions by maintain long-term groups with non-kin. Indeed, within the non-breeding grounds, grouping can help with predator detection and competition for prime feeding areas, thus increasing fitness and reducing stress levels [33]. Not only can this increase survival, but it can also help maintain a better body condition during migration and increase later reproductive success. During migration, flocking can increase navigational accuracy [7,42] either through social learning,

where experienced individuals guide less experienced individuals [2], or through collective learning, where groups pool their knowledge to generate better migratory decisions than solitary individuals [43].

Whether through collective or social learning, being able to transfer information within a group to identify new non-breeding sites, allows birds to respond to environmental changes [2,7]. This could potentially be the case for our study population whose migratory range has rapidly expanded, with new breeding and non-breeding sites appearing in Europe and the Congo Basin respectively ([40]when birds were previously only known to migrate to Western and South Eastern Africa [41]). Given the stability of these non-kin groups, and the rapid emergence of new migratory routes, it is possible that social transfer of information could, in combination with phylogenetic plasticity, be affecting this change. Indeed, though phylogenetic plasticity can allow populations to change migratory routes over generations, behavioural plasticity can allow these changes to occur within the lifespan of an individual.

Overall however, migratory birds are declining more severely than non-migratory birds [44]. Given the current rate and extent of anthropogenic driven changes, adaptability could be key in averting population declines. Disentangling the relative roles of genetic, social and environmental factors in migration could help understand how collective decision-making affects large-scale movements, and how new migratory routes might (or might not) arise from social transfer of information, and thus how adaptable a species might be to a changing environment.

Conclusions

In conclusion, we find that (i) birds from the same colony do not always follow the same migratory routes but will in fact join with birds from nearby colonies post-breeding to (ii) form groups which migrate together. Groups are generally (iii) stable during migration. However, if groups separate, they will reunite in the non-breeding grounds to form dynamic groups which repeatedly forage together, sometimes separating for 1-5 days at a time before migrating back to the breeding grounds together. Most surprisingly, these groups showed (iv) no age or sex structure and consisted of non-kin. Our research is the first to show such behaviour between migratory non-breeding non-kin bird groups, displaying rare spatiotemporal group dynamics more often observed in mammals [17,19].

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211 **Author contributions**

212 FL came up with the initial concept of the paper, KLDA performed the analysis and wrote the first
213 draft of the manuscript, TE and SH collected data, SL and KLDA wrote code. All authors developed
214 the concepts of the paper and edited final version of manuscript.

215

216 **Declaration of Interests**

217 The authors declare no competing interests.

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219 **References**

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STAR Methods

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead contact, Kiran Dhanjal-Adams (kiran.dhanjal.adams@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

During July 2015 and 2016, we fitted 77 and 92 multi-sensor loggers (Figure S1; respectively; SOI-GDL3pam, Swiss Ornithological Institute) on European bee-eaters (*Merops apiaster*). These loggers recorded both light for geolocation, and atmospheric pressure for altitudinal changes. Due to the nature of the tag, individuals needed to be recaptured for data to be downloaded. All birds were tagged and recaptured in two breeding colonies (51°36'N, 11°93'E) belonging to a wider population which has established in Saxony-Anhalt since 1990, in the northern expanding front of the species' distribution in Germany [45]. With roughly 30 breeding pairs in 2003, the population is currently estimated at 800 breeding pairs [40], which migrate to non-breeding sites spread out between Gabon and Angola [40]. Being at the expanding front of the species distribution, this population has not yet reached carrying capacity. Breeding is therefore less likely to fail for individuals in this population, than for more southern populations, reducing the pool of potential helpers and therefore the number of cooperatively-breeding groups [46]. In fact, none of the recaptured birds in 2016 and 2017 had bred cooperatively in 2015 and 2016.

We aimed to tag an even mix of males and females, both second year and older adults, with individuals that bred together and individuals that did not breed together. Due to high dispersal and mortality, we did not tag any first-year juveniles. For the same reasons, we recaptured 10 birds in July 2016, and 19 in July 2017 (Table S1). Unfortunately, we were not able to recapture any birds which had bred together in the previous year, though some birds which had not bred together when fitted with loggers did breed with another tagged bird when recaptured (Table S1). Finally, none of the recaptured individuals were caught together within the same burrow in the years before the analysis (roughly 80% of birds have been ringed since 2003 and >95% since 2007), indicating they were not likely kin, or previously pair-bonded.

METHOD DETAILS

Geolocation

Light-intensity data were recorded at 5 minute intervals and analysed using a threshold method [47]. Sunrise and sunset events were identified (using the *R* package *TwGeos* [48] on log transformed light

data) and a threshold of 0 (arbitrary units). To define the error distribution of sunrise/sunset times caused by shading (e.g. clouds, habitat) we used the recordings from the beginning of the time series (a day after it was fitted on the bird), until the day before the start of migration (as defined in the next section using *change point*) as a calibration dataset with known location. The defined error distributing (gamma density distribution with shape = 3.83 ± 1.49 and rate = 0.23 ± 0.07) was then used within the R package *SGAT* [49] to refine track estimates. *SGAT* provides a Bayesian framework which allows us to combine prior information on (i) twilight error distribution, (ii) the flight speed distribution (defined using a relaxed gamma distribution of shape = 1.6 and rate = 0.27), and (iii) a spatial probability mask to ensure birds spend more time on land than at sea with the location estimates. This allows us to refine locations based on a Markov chain Monte Carlo (MCMC) simulations and provide a probability distribution around each estimate (two locations per day). The first and last location was fixed to the breeding site because all birds were captured and recaptured at the same breeding colony (51°36'N and 11°93'E). We first ran a *modifiedGamma* model (relaxed assumptions) for 250 iterations to initiate the model, before tuning the model with final assumptions/priors (three runs with 300 iterations). Finally, the model was run for 2000 iterations to ensure convergence.

We then investigated the overlap in the spatial distribution of tracks between all birds. Distributions were first converted to raster format, and grid cell values normalised to sum up to one. We then defined the overlap as the sum of the minimum values of each overlapping grid cell. This was performed for overall tracks, and for each migratory stage, between pairs of birds where tracks were available.

Ambient air pressure

Ambient air pressure data were recorded at 30-minute intervals. Indeed, air pressure varies as a function of weather conditions, geographic location and altitude, creating a unique signature for each bird at a fine temporal resolution. Because background variations in air pressure linked to weather do not exceed 8 hPa per day and 1hPa per hour (Figure S4), while variations in air pressure linked to changes in altitude (i.e. bird flight) range from 2-331 hPa per day and 1-205 hPa per hour (Figure S4), we can identify individual flight events - when they started and stopped, as well as altitudinal variations (Figures 2 and S4). Assuming a starting pressure of 1000 hPa at 20°C for example, the hourly range in pressure during flight of 1-205 hPa is equivalent to an hourly change in altitude of 8.6-1968.6 m. Thus, not only is the range of altitudinal changes observed in these birds high, but so is the rate.

Indeed, bee-eaters are diurnal migrants and preferentially soar-glide as a migratory strategy by manoeuvring from one thermal updraft to the next [36], creating a unique pattern of altitudinal changes at a fine temporal resolution (Figure 2). It is therefore possible to identify whether two birds

make the decision at the same time to fly or not fly, to go up or down, and how high or low to fly (Figure S2A-E). We assume that if two individuals repeatedly make the same decision at the same time during daytime (Figure 2), especially over weeks or months, then this decision is shared between the two individuals. Indeed, bee-eaters often display complex social interactions, breeding cooperatively [24], mobbing predators, preening and foraging socially (even with other species [26]), as well as socialising on migration with flock members [29].

QUANTIFICATION AND STATISTICAL ANALYSIS

We used a hidden Markov model (HMM) to identify birds with synchronised flight decisions. The HMM classified three variables derived from daytime atmospheric pressure (daytime was identified using the light data by applying the *twilightCalc* function in the package *Geolight* [50]). Firstly, we derived the correlation in atmospheric pressure at time t minus atmospheric pressure at time $t+1$. This variable represents the synchronisation in the direction and amplitude of flight. Secondly, we derived the correlation in raw atmospheric pressure. This variable is broadly used to find synchronised birds (similar to the latter, but does not distinguish well when birds might have a similar overall patterns, but may not be going in the same direction at a fine temporal scale as seen in Figure 2C). Finally, we derived the median absolute pressure difference between pairs of birds. This is used to ensure that birds in different pressure zones are not classed as together, and that birds whose pressure varies in parallel are classed similarly.

We then used the R package *depmixs4* [51] to classify the three variables into 5 states assuming a gamma distributions for each of the pressure-derived variables. These can be seen in figure S2A with (i) “high difference in pressure between birds”, (ii) “medium pressure difference, low correlation in raw pressure and altitudinal changes”, (iii) “medium pressure difference, high correlation in raw pressure and altitudinal changes”, (iv) “low pressure difference, low correlation in raw pressure and altitudinal changes”, (v) “low pressure difference, high correlation in raw pressure and altitudinal changes”. The latter was used to class birds as together (Figure S2). Thus, if birds are in a same pressure region, have similar pressure patterns, and are synchronise in the direction in which they are flying, then we assume that the decision to change altitude is synchronised, and that birds must be within the same flock.

It is important to note that although daytime pressure was used to infer coordinated decisions, it cannot be directly correlated to geographic proximity. Indeed, even birds nesting within 500 metres of each other in the same breeding colony were not always classified as flying (and therefore foraging socially) together during daytime hours (Figure 3A). In fact, we observed similar numbers of foraging interactions between birds from different colonies (6 km apart) as from birds within the same colony. This is consistent with known bee-eater behaviour, where birds forage socially within 3 to 12 km from the colony [52], sometimes even with other bee-eater species [26]. In fact, many birds from our study

have been captured in both colonies, even within the same breeding season (e.g. OO in Table S1). The fact that birds from within the same colony are classified as apart despite their close proximity indicates that the classification is not overestimating “togetherness” as a result of geographic proximity, or weather (Figure S2E and F).

We then classified the air pressure timeseries for each birds into periods of “migration” and “non-migration”, using the R package *changept* [53]. This allowed us to identify change points where the standard deviation in ambient air pressure changed state (i.e. changes in state: “not migrating” and “migrating”). Once migration periods were identified for each bird, we defined the overall migration period from when the first bird started migrating to when the last bird stopped migrating. Using these periods, we then broke the air pressure readings for each bird into life cycle stages for the analysis (breeding before migration, southward migration, non-breeding, northward migration and breeding after migration).

DATA AND SOFTWARE AVAILABILITY

Code for geolocation and raw pressure data visualisation can be viewed as an R markdown html document at <http://doi:10.17632/wrwhbbptg8.2> . Interactive pressure graphics allow the user to explore the raw pressure measurements by zooming in along both the x and y axes by clicking and dragging the mouse over different regions. Double-clicking allows the user to zoom out again. Furthermore, modelled track estimates, raw light and pressure data are stored in Movebank project number 502110670 and are available upon request (http://www.movebank.org/panel_embedded_movebank_webapp?gwt_fragment=page=studies,path=study502110670)

Figures

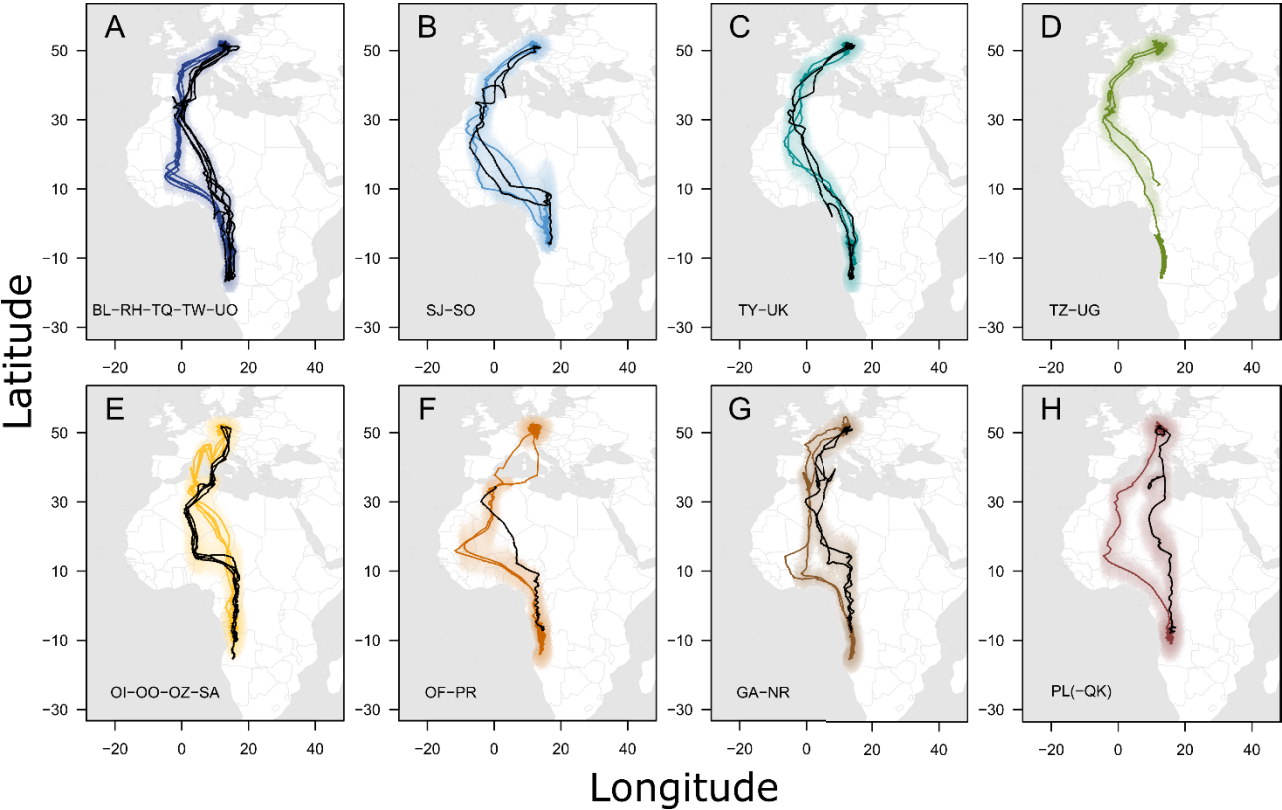


Figure 1. Overlap in geolocation estimates for (A) group1: BL-TH-TQ-TW-OU, (B) group 2: SJ-SO, (C) group 3: TY-UK, (D) group 4: TZ-UG, (E) group 5: OI-OO-OZ-SA, (F) group 6: OF-PR, (G) group 7: GA-NR and (H) group 8: PL-QK. Coloured tracks represent migration southwards and black tracks migration northwards. Note that QK did not record light, so we have no geolocation estimate for it. Individuals named TW, TZ, UG and OF stopped recording light during southward migration. Panels A, B, C and D were all tagged 2016-2017 and E, F, G and H in 2015-2016. See also Figure S1.

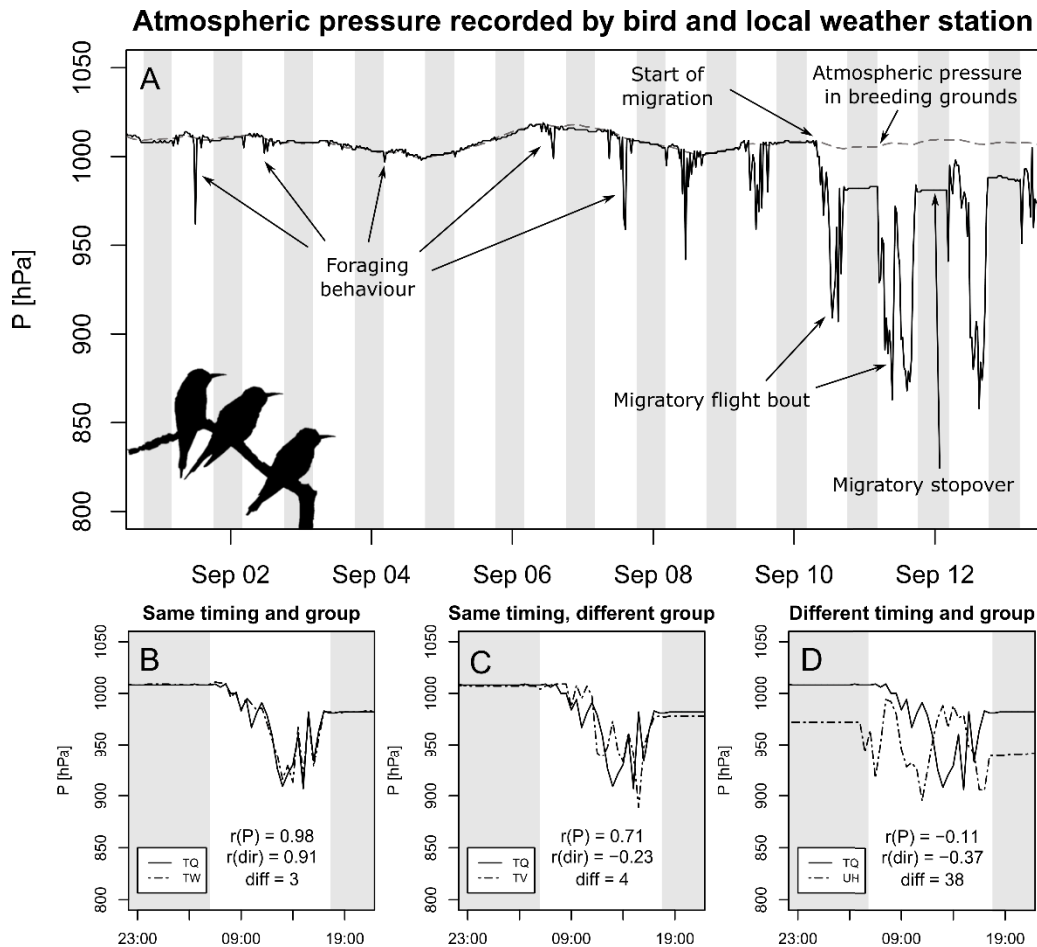


Figure 2. Examples of raw air pressure measurements (P) in hectopascals (hPa) for bird (A) TQ in September 1st -13th 2016 compared with pressure for (B) TW, (C) TV and (D) UH on September 10th. Grey shading represents nighttime periods for TQ derived from geolocation. We only consider pressure during daytime because this is the period when birds are actively changing altitude and therefore less likely to be similar when birds are not together. Indeed, looking at raw atmospheric temperature measurements in panel a for TQ (in black), we can see that they follow the same background pressure variations recorded at the local weather station (in red) until the start of migration. The change in atmospheric pressure during flight bouts is much higher than that of background fluctuations in atmospheric pressure driven by weather (Sep 1st -9th in panel a) or by geography and topography (Sep 10-11th). It is therefore possible to distinguish between pressure changes caused by flight (during daytime), weather (during nighttime) and geography (from one night to the next). Birds classified as migrating together (B) are birds whose raw pressure measurements are highly correlated [$r(P)$], whose direction and amplitude of altitudinal changes is correlated [$r(\text{dir})$] and whose difference in pressure measurements between birds is low [diff]. High synchronisation occurs between individuals migrating together (B). However, birds can experience similar background pressure conditions while following similar migratory routes, without having synchronised behaviour (C). Finally, some birds record completely different atmospheric pressure, indicating their migratory behaviours are different (D). See also Figure S2.

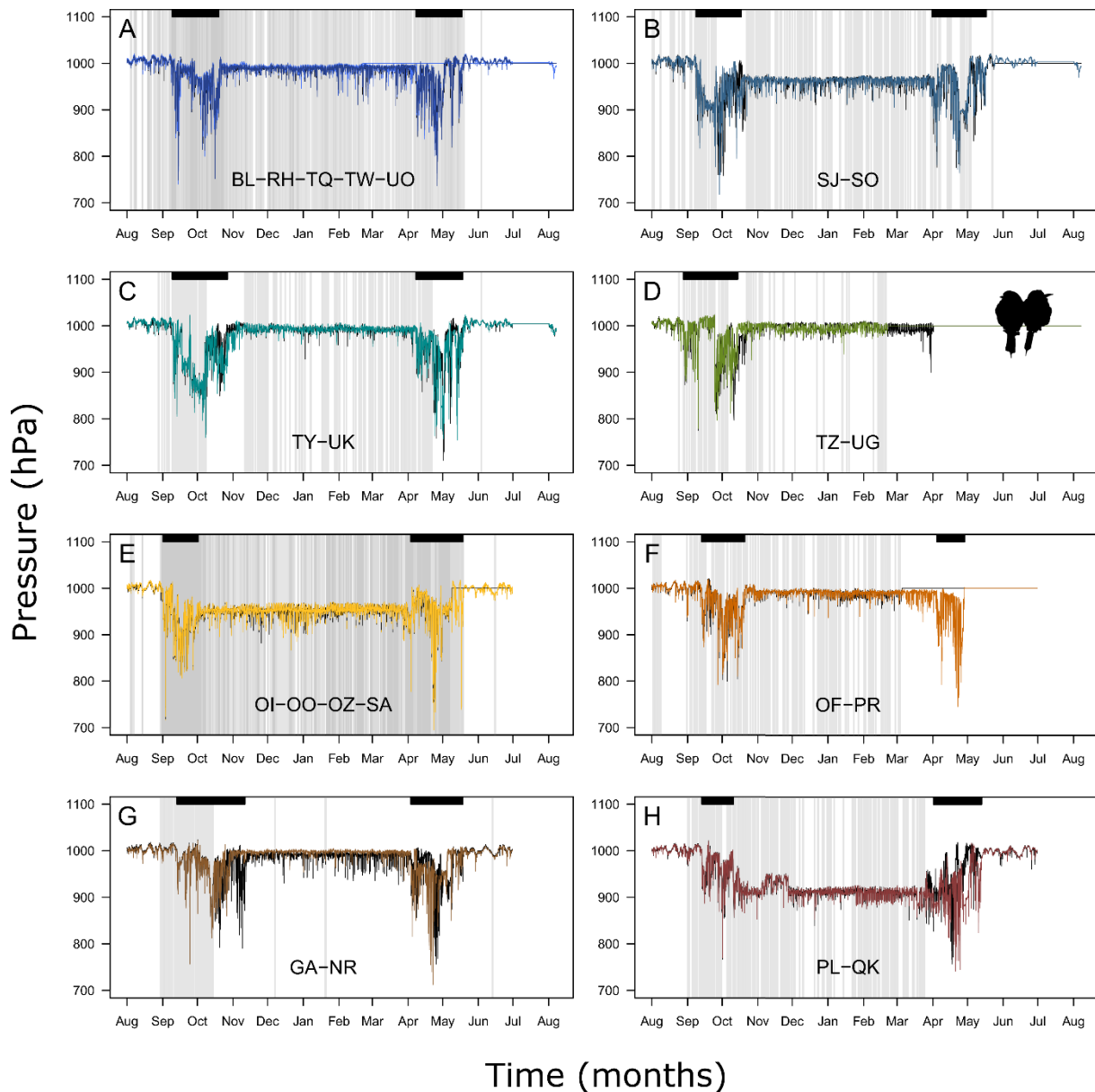


Figure 4. Raw air pressure measurements in hectopascal for all social groups across the annual cycle. These illustrate fission-fusion for (A) group1: BL-TH-TQ-TW-OU, (B) group 2: SJ-SO, (C) group 3: TY-UK, (D) group 4: TZ-UG, (E) group 5: OI-OO-OZ-SA, (F) group 6: OF-PR, (G) group 7: GA-NR and (H) group 8: PL-QK, where the grey background represents periods when the birds were classified as “together”. For A and E, there are 5 and 4 birds respectively within the groups, and darker grey represents days when all birds are classed as together, and lighter grey when only some birds within the group are classed as together. Black bars represent migratory periods, with the left bar indicating south (post-breeding) migration, and the right bar north (pre-breeding) migration. Note that A, B, C and D were tagged in 2016-2017, and E, F, G and H in 2015-2016. See also Figures S3 and S4.

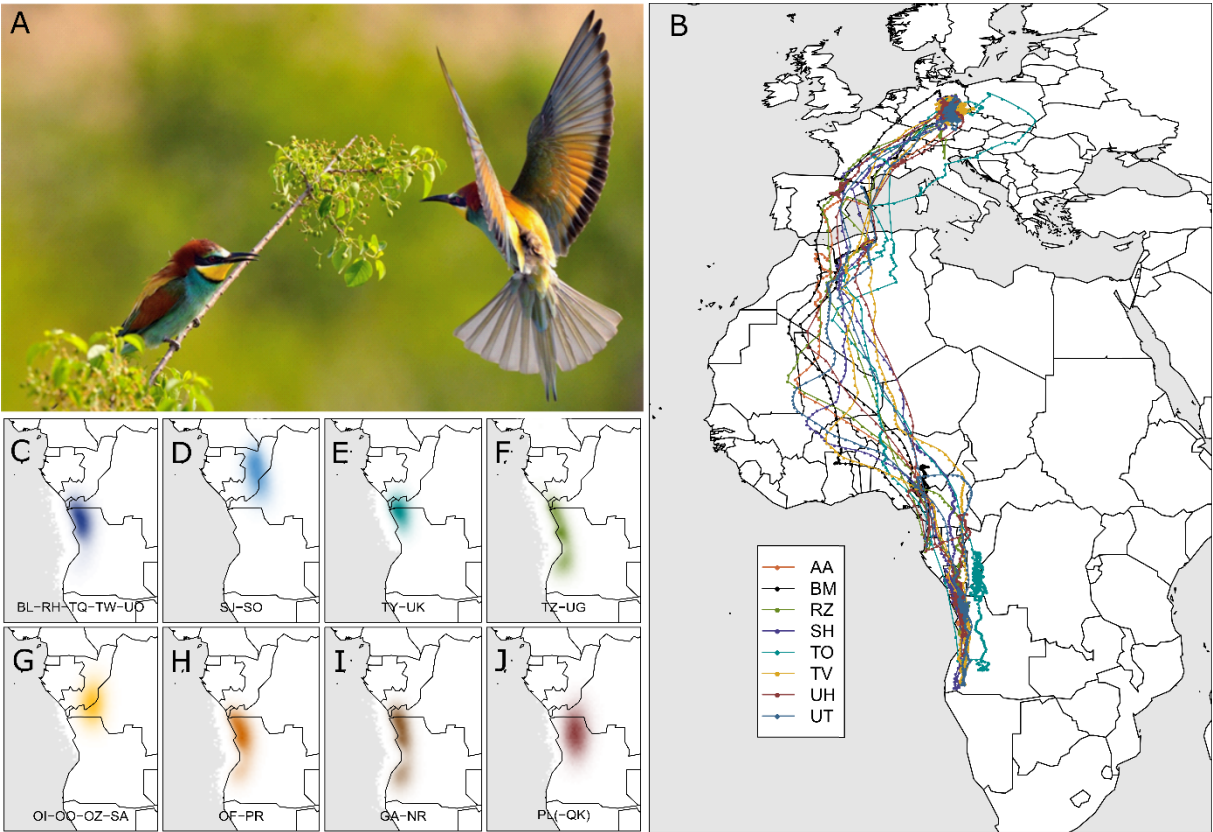


Figure S1. European bee-eater migratory patterns and non-breeding ranges as revealed by geolocation, Related to Figure 1 and STAR Methods. **A** Two European bee-eaters (*Merops apiaster*) from this study. Individual on the right has been fitted with a 1.4g multi-sensor logger (SOI-GDL3pam, Swiss Ornithological Institute) Copyright: Bernd Sekka, image used with permission. **B** Median geolocation estimates for birds which did not show groups with another tagged bird: AA, BM, RZ, SH, TO, TV, UH and UT. All were tagged between July 2016 and July 2017. Note that the 95% confidence intervals of tracks are not presented. Note also that equinox occurs just as birds start migrating northwards, pulling the track south in the non-breeding grounds. **C.** Non-breeding distribution of group 1: BL-RH-TQ-TW-UO; **D** Non-breeding distribution of group 2: SJ-SO. **E** Non-breeding distribution of group 3: TY-UK. **F** Non-breeding distribution of group 4: TZ-UG. **G** Non-breeding distribution of group 5: OI-OO-OZ-QK. **H** Non-breeding distribution of group 6: OF-PR. **I** Non-breeding distribution of group 7: GA-NR and **J** non-breeding distribution of group 8: PL-QK.

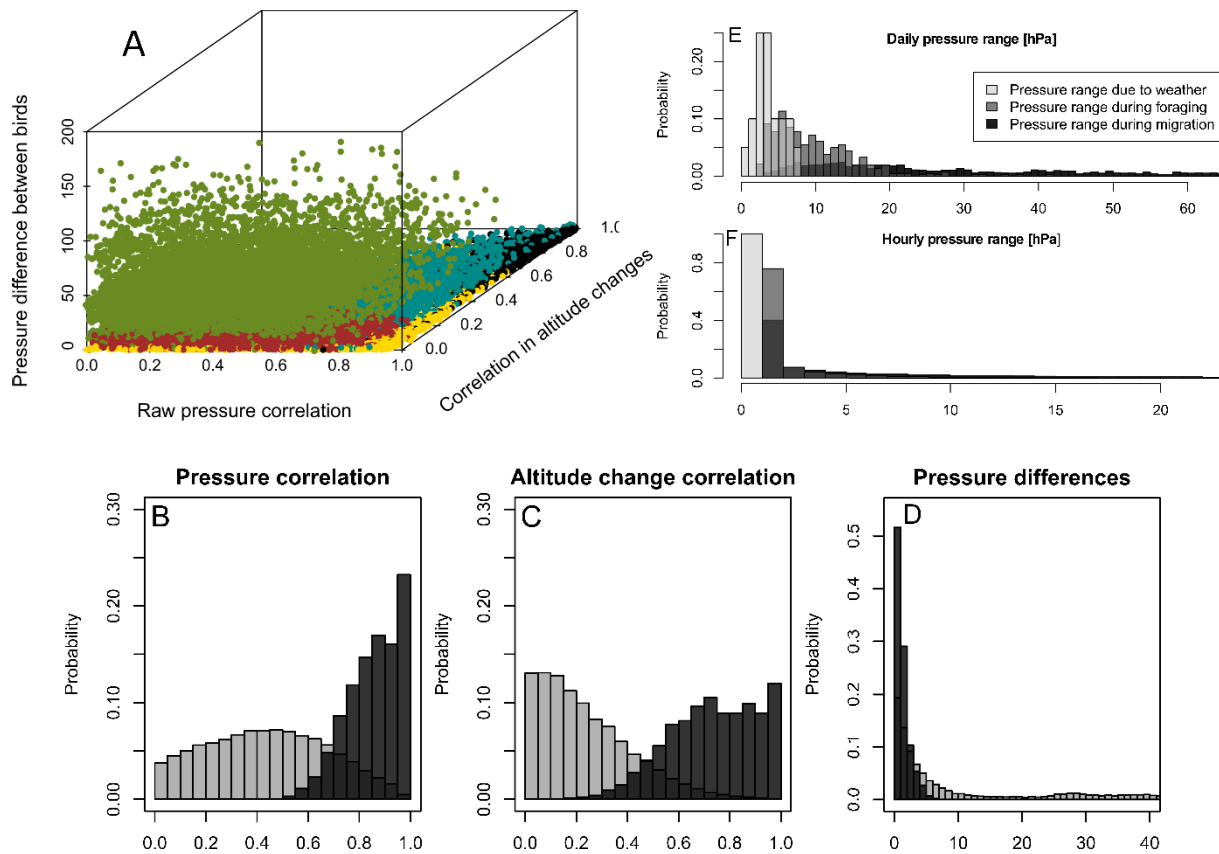


Figure S2. Classification output from the hidden Markov model, Related to STAR Methods and Figure 2. **A** We used 5 classes to separate the data (green: “high difference in pressure between birds”, red: “medium pressure difference, low correlation in raw pressure and altitudinal changes”, blue: “medium pressure difference, high correlation in raw pressure and altitudinal changes”, yellow: “low pressure difference, low correlation in raw pressure and altitudinal changes”, and black: “low pressure difference, high correlation in raw pressure and altitudinal changes”). Birds were classified as “together” from black points in panel A, when they had **B**) a high correlation in raw daily pressure between birds (to determine if birds have similar pressure patterns), **C**) a high correlation in directional pressure changes (to determine whether they make the similar movement decisions at the same time) and **D**) low median absolute pressure difference between birds (so that birds in different pressure zones are not classed as together). **E and F** represent the density distribution of pressure ranges linked to background weather, foraging and migration. Throughout the day (panel E), weather never causes a change bigger than 8 hPa, foraging 2-42 hPa and migration 3-331 hPa. At an hourly basis (panel F), weather never causes a change bigger than 1 hPa, while foraging and migration always change by at least 1 hPa ranging to 37 hPa during foraging and 205 hPa during migration.

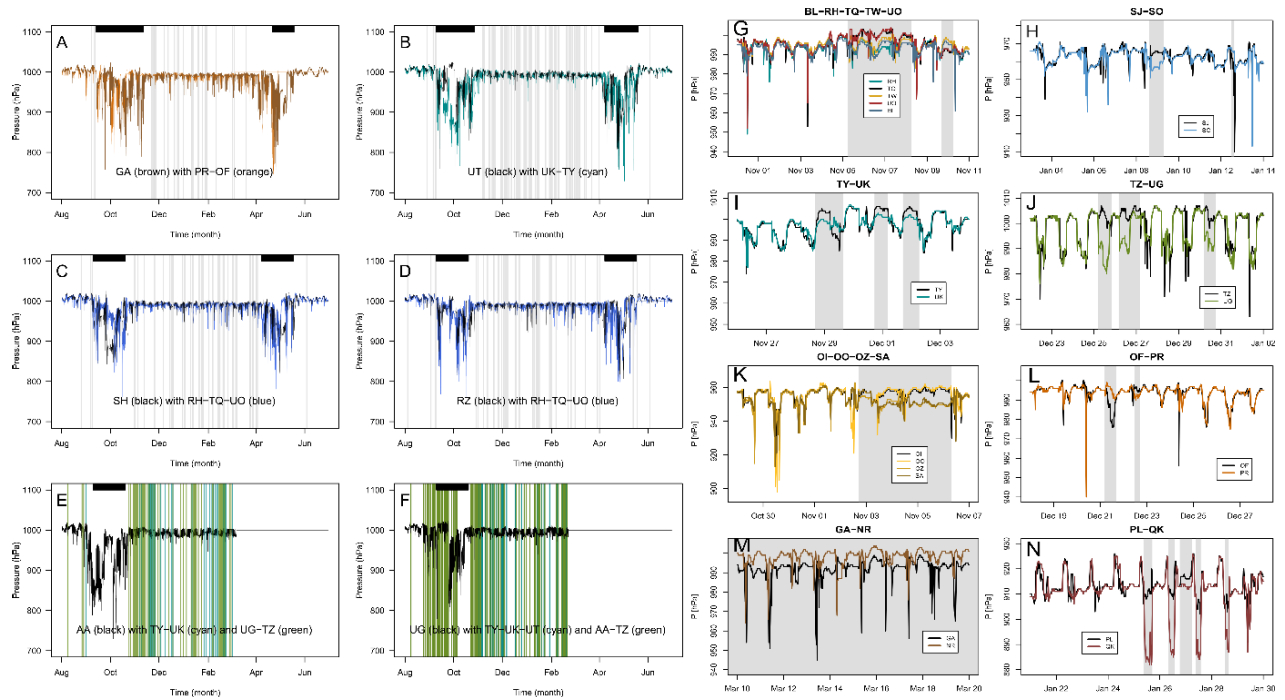


Figure S3. Raw air pressure measurements in hectopascal for birds that were together (left panel) or apart (right panel), Related to Figures 3 and 4. Left panels (A-F) illustrate fission-fusions in the breeding and non-breeding grounds for (A) GA (group 7) with OF-PR (group 6), for (B) UT with TY-UK (group 3), (C) SH with RH-TQ-UO (group 1) and (D) RZ with RH-TQ-UO (group 1). For A-D, grey represents periods when the bird joins another group. Panels E and F represent birds AA and UG who on some occasions are together with individuals from group 3 (cyan) and sometimes group 4 (green). Note there are times when both groups overlap. Right panels (G-N) show examples of raw air pressure measurements (P) in hectopascal (hPa) for all social groups during the non-breeding season. The examples illustrate fission-fusion for 1: BL-RH-TQ-TW-UO (panel G), 2: SJ-SO (panel H), 3: TY-UK (panel I), 4: TZ-UG (panel J), 5: OI-OO-OZ-QK (panel K), 6: OF-PR (panel L), 7: GA-NR (panel M) and 8: PL-QK (panel N). Different pressure measurements indicate that birds are no longer experiencing the same weather conditions while also no longer changing altitude in unison, and are therefore no longer together (grey background). For example, in N, PL and QK roost together at a higher altitude (910 hPa i.e. between 919 and 945m according to the range of known temperatures in the region) than they forage (920 hPa i.e. 825-849m). During separation on January 25th, QK then forages at a higher altitude, but returns to roost with PL. Note that G-J were tagged in 2016-2017, and I-N in 2015-2016.

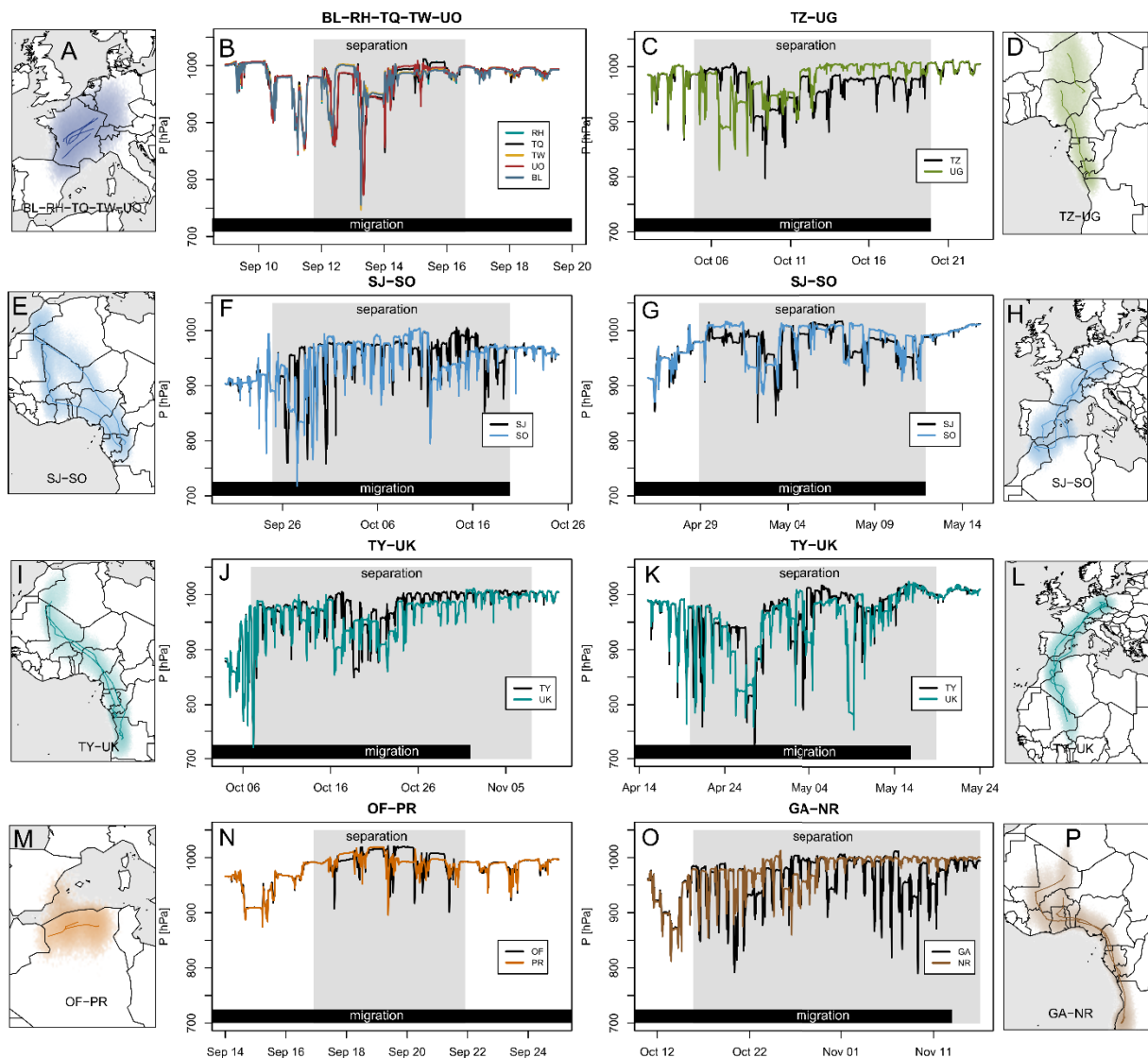


Figure S4. Geolocation and raw pressure measurements during periods of separations, Related to Figures 3 and 4. Outer panels. Geographic location of birds during periods of separation as estimated by geolocation by light. Group fission occurred during **A** south migration for BL-TH-TQ-TW-OU (group1), **D** south migration for TZ-UG (group 4), **E** south migration for SJ-SO (group 2), **H** north migration for SJ-SO (group 2), **J** south migration for TY-UK (group 3), **L** north migration for TY-UK (group 3), **M** south migration for OF-PR (group 6) and **P** south migration for GA-NR (group 7). Shading represents the 95 confidence intervals of geolocation estimates, and lines the median geolocation estimate. Note that geolocation lacks precision, especially during equinox (relevant for a and g), thus these figures only provide a rough estimate of bird locations when separating. **Inner panels:** Raw air pressure measurements in hectopascals (hPa) for social groups which separated during migration. **B panel:** BL-TH-TQ-TW-OU (group1), **C panel:** TZ-UG (group 4), **F and G panels:** SJ-SO (group 2), **J and K panels:** TY-UK (group 3), **N panel:** OF-PR (group 6) and **O panel:** GA-NR (group 7). Migration periods can be identified based on the relative change in ambient air pressure. Indeed, changes in altitude during flight will cause pressure to decrease substantially relative to breeding and non-breeding residency seasons, allowing us to identify migratory periods (horizontal black bar). Different pressure measurements indicate that birds are no longer experiencing the same weather conditions while also no longer changing altitude in unison, and are therefore no longer migrating together (grey background). Note that A, B, C, E, H and G all separated during south migration, while d and f during north migration. Finally, A, B, C, D, E and F were tagged in 2016-2017, and G and H in 2015-2016.

ID	Sex	Age	Release	Recapture	Pressure last record	Light last record	Release nest	Release colony	Recapture nest	Recapture colony	Group
RZ	M	2	11/07/16	15/07/17	recapture	recapture	21	B	51	A	0
SH	M	2	11/07/16	16/07/17	21/06/17	21/06/17	28	A	3	A	0
OO	F	2	19/07/16	15/07/17	recapture	recapture	60	B	45	A	0
TV	M	2	10/07/16	12/07/17	recapture	recapture	21	A	19	A	0
UH	M	>2	11/07/16	13/07/17	recapture	recapture	33	B	57	B	0
UT	F	2	09/07/16	13/07/17	recapture	recapture	1	B	72	B	0
AA	F	>2	11/07/16	11/07/17	02/03/17	02/03/17	32	B	13	B	0
BM	F	>2	12/07/16	13/07/17	recapture	recapture	34	B	68	B	0
RH	M	2	10/07/16	14/07/17	recapture	recapture	25	A	27	A	1
UO	M	>2	11/07/16	14/07/17	recapture	recapture	31	B	28	A	1
TQ	F	>2	12/07/16	17/07/17	14/05/17	14/05/17	41	A	28	A	1
TW	M	>2	13/07/16	14/07/17	25/02/17	25/02/17	63	B	37	A	1
BL	F	>2	11/07/16	14/07/17	22/06/17	22/06/17	18	A	26	A	1
SJ	M	2	10/07/16	13/07/17	19/05/17	19/05/17	22	A	49	B	2
SO	F	2	13/07/16	13/07/17	recapture	recapture	61	B	54	B	2
TY	F	2	10/07/16	13/07/17	recapture	recapture	14	A	77	B	3
UK	F	>2	13/07/16	13/07/17	recapture	recapture	51	B	85	B	3
TZ	F	2	11/07/16	13/07/17	28/03/17	28/03/17	36	A	80	B	4
UG	M	2	11/07/16	14/07/17	22/02/17	22/02/17	22	B	83	B	4
OI	M	2	16/07/15	11/07/16	recapture	recapture	50	A	41	A	5
OO	F	2	13/07/15	12/07/16	recapture	recapture	31	A	41	A	5
OZ	M	>2	12/07/15	12/07/16	08/05/16	08/05/16	28	A	47	A	5
SA	F	>2	13/07/15	15/07/16	recapture	recapture	33	A	53	A	5
OF	M	>2	12/07/15	11/07/16	04/03/16	04/03/16	22	A	24	A	6
PR	M	2	12/07/15	11/07/16	28/04/16	28/04/16	20	A	40	A	6
GA	F	2	15/07/15	11/07/16	recapture	recapture	39	A	24	B	7
NR	F	2	15/07/15	19/07/16	recapture	12/07/16	41	A	50	A	7
PL	M	2	11/07/15	10/07/16	recapture	recapture	no data	A	4	A	8
QK	M	2	15/07/15	10/07/16	recapture	no data	52	A	7	A	8

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599 **Table S1. Information pertaining to each tagged bird, Related to STAR Methods.**