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Communication

Goose parents lead migration V

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Many migratory animals travel in large social groups. Large, avian migrants that fly in V-formations were proposed do so for energy saving by the use of up-wash by following individuals and regularly change leadership. As groups have been rather homogeneous in previous work, we aimed to explore leadership and its flight mechanics consequences in an extremely heterogeneous case of social migration, namely in spring migration of goose families. In families the experience of group members differs strongly and inclusive fitness may be important. We successfully collected overlapping spring migration tracking data of a complete family of greater white-fronted geese *Anser a. albifrons* and extracted leadership, flapping frequency and wind conditions in flight. Our data revealed V-formations where one parent was flying in front at all times. Although the father led the family group most of the time, he did not flap at higher frequency while doing so. In contrast, the mother flapped faster when leading, possibly because she experienced less supportive wind conditions than when the father led. We argue that in heterogeneous, social groups leadership might be fixed and not costly if supportive environmental conditions like wind can be used.

Keywords: flight mechanics, goose family behaviour, group migration, leadership, V-formation flight

Introduction

Migratory animals must optimise their energetic and cognitive performances during the yearly long-distance travels (Milner-Gulland et al. 2011). Behavioural adaptations like the adjustment of migration timing (Gauthreaux et al. 2005, Kölzsch et al. 2016) and routes (Bohrer et al. 2012) or the formation of social groups (Berdahl et al. 2018, Flack et al. 2018) allow them to minimise energy expenditure and to profit from favourable atmospheric conditions and each other's experience (Couzin et al. 2005, Kemp et al. 2010, Sapir et al. 2010).

Large, heavy bird species depend strongly on environmental support, because the flight costs of powered flapping flight increase with body mass (McWilliams et al. 2004, Elliott 2016). To overcome this limitation, some birds utilize vertical air currents (updrafts) in a soaring–gliding fashion to travel with minimal energy expenditure

(Duriez et al. 2014). Others travel in formation flight to reduce movement costs through aerodynamic effects. Theoretical and empirical studies have shown that V-formations can improve flight efficiency because birds position themselves in a way that they benefit from up-wash caused by the preceding bird (Lissaman and Shollenberger 1970, Hummel 1983, Portugal et al. 2014). However, the leading bird in a formation does not experience this advantage, because it cannot position itself in an up-wash. This disadvantage can be mitigated by two different strategies.

In flocks of unrelated individuals, birds are expected to swap positions frequently among all group members, as observed in a group of juvenile bald ibises during their human-led migration (Voelkl et al. 2015). In flocks composed of closely related birds, we may, however, observe a different, more fixed strategy as the leading bird can still gain indirect fitness benefits that outweigh leading costs. Such cooperation based on kin selection may be more common in species flying in small family groups like cranes, swans or geese (Scott 1980, Alonso and Alonso 1993, Ely 1993, Voelkl and Fritz 2017). Because juveniles can be affected more strongly by the strenuous journeys and are less experienced flyers (Sergio et al. 2014) it might be more essential for them to save energy by following and relying on the guidance of a leading parent.

Here we examined leadership patterns in an entire family of six greater white-fronted geese *Anser a. albifrons* using GPS/acceleration data. Because the geese have to migrate through regions with high hunting pressure (Mooij 1997) and some families separate already during winter or early spring, collecting migration flight data of a complete family that answers questions concerning social organisation is challenging. We succeeded in exploring the cooperation strategy and its energetic consequences of a family of freely-migrating geese during its approximately 2300 km long journey. We hypothesized that inexperienced juvenile geese would most of the time be guided by one of their parents. More specifically, we predicted that adults and juveniles differ in their energy expenditure because of differences in experience and flight ability. We argue that in heterogeneous groups such as a family of social migrants, leadership is not shared equally among all group members, but mainly taken by the parents.

Material and methods

Goose family GPS/accelerometer tracking

With help from the Dutch Association of Goose Catchers we were able to catch four complete families of white-fronted geese (8 adults and 15 juveniles) in the south of the Netherlands between 15 Nov 2014 and 15 Dec 2014. Using their unique system of catching wild geese with families of tame decoy geese, we identified family bonds from behaviour just prior to catching, which was later confirmed by DNA analyses (M. Wink, unpubl.). All tracked juveniles were genetic offspring of the respective pair of parents. Birds were sexed by cloacal examination and age was determined

by feather and bill characteristics. We have selected the four families with many (3–5) juveniles and all members above 1800 g body weight to minimize discomfort. All individuals of the families were equipped with a simple numbered neckring for identification by observation and a GPS/accelerometer transmitter with GPRS download (eobs GmbH, 45 g) that was attached using a Teflon/Tygon/Nylon harness (Fig. 1c, Lameris et al. 2017). Handling the geese was done in accordance with all relevant guidelines and regulations and experimental protocols were approved by the Animal Welfare Committee of the Royal Netherlands Academy of Arts and Sciences (DEC NIOO13.14).

Two of the four goose families stayed together into spring migration, but only one of them provided enough data for proper analysis. The positions of this family were our main data set; the few additional ones of the second family were analysed to compare to our findings (Supplementary material Appendix 1). We analysed flight data of spring migration 2015 that was defined as the time between 20 March and 30 June 2015 where the GPS positions indicated a height above ground of at least 165 m and ground speed of more than 10 m/s (Kölzsch et al. 2016). During this time GPS positions were collected in 1 Hz bursts of 60 s every half hour and acceleration at 20 Hz for about 5 s every 10 min, if tag energy levels permitted. The GPS tracks are uploaded to Movebank (www.movebank.org), available in the study 'Greater white-fronted goose family migration flight' and published in the Movebank Data Repository – doi:10.5441/001/1.ms87s2m6 (Kölzsch et al. 2020).

Data selection for flight formation analysis

The focus goose family started their migration from the Netherlands with their four juveniles (two male, two female) on 23 March 2015 (Fig. 1a). The selected data set for the flight leadership and energetics analyses were a subset of 50 GPS burst (of lengths of 8–59 GPS positions, median 58) after this date. All selected positions had an absolute horizontal location error of less than 15 m; the average was 2.3 m. However, relative horizontal position error is usually much lower (Wilson et al. 2013), given that the tags were oriented similarly (circular correlation of GPS directions of all pairs of tags: r = 0.997). For each of the selected GPS positions a time-overlapping accelerometer burst was available. Three of the juveniles were shot or predated at the end of the route (J1a 19/5/2015 Russia; J1b 31/03/2015 Poland; J1d 20/4/2015 Belarus).

Flight formation and leadership extraction

For each burst of GPS flight data, the positions of all family members were aligned by time and only timestamps selected where both father and mother provided a position, totalling 9539 GPS positions. For each timestamp, the GPS positions (transformed to UTM zone) of all family members were shifted and turned in relation to the father or mother, respectively, so that their flight direction would point upwards and distances between family members were conserved.

Figure 1. Spring migration tracks of a goose family. Positions and times of analysed GPS bursts. (a) Julian dates of 2015 indicating times of analysed flight data by individual; M (blue) indicates the father, F (red) the mother and J (black) the juveniles with their sex noted in brackets behind (m – male, f – female). (b) Migration tracks (lines) with positions of analysed flight GPS positions (dots). Multiple lines indicate where single chicks had split off the family group. (c) Photograph of a tagged family before release in the Netherlands. The map (b) was created with R 3.4.3, package 'ggmap' using as background googlemaps (see https://developers.google.com/maps/documentation/maps-static/intro).

This transformation allowed the extraction of lateral and longitudinal displacements in flight direction between the two parents and the juveniles.

The leading parent was determined as the most forward parent in flight direction for each timestamp and the positions of the juveniles in relation to the leading parent were determined. This allowed extraction of longitudinal and lateral displacements as well as the angle between leader and follower. Those measures were especially informative for direct followers (<3 m behind leading parent) (Voelkl and Fritz 2017), as they allow conclusions about flight mechanics that possibly relate to energy saving.

Flight mechanics, travel speed and tail wind

To evaluate if leadership had an effect on flight mechanics, we determined overall dynamic body acceleration (ODBA, in units of 'g' where 1 'g' = 9.81 m s^2) (Wilson et al. 2006) and wing beat frequency (Pennycuick 1996) (Supplementary material Appendix 1) as measures of flapping frequency (Bishop et al. 2015, Elliott 2016). As the two measures were correlated (Supplementary material Appendix 1 Fig. A1) and wing beat frequency had extremely low variability (due to tag settings), we decided to use ODBA for our main conclusions. These did not differ from conclusions to be drawn from analyses of wing beat frequency (Supplementary material Appendix 1 Fig. A2).

All analysed GPS positions were annotated with ODBA allowing for a delay of up to 15 min (average delay: 10.4 min). As this is not optimal, it is known that geese migrate in long stretches of time (Kölzsch et al. 2016), so likely stay aloft during the delay. We compared ODBA of the leading parent to all family members that followed them, distinguishing between mother versus father leading. As flight mechanics should depend on body mass (Hedenström 2012), we explored if body mass (at catching) had a consistent relation to flight ODBA. Furthermore, we annotated the analysed GPS positions with ground-level ECMWF wind reanalysis data (Dodge et al. 2013) and calculated tail wind (Safi et al. 2013), which was finally set into relation to ODBA and air speed of the mother or father when leading versus directly following juveniles. All relationships were tested by generalised linear mixed models (GLMM, R-package 'lme4') with individual ID as random factor. Model estimates indicate average deviations of the target variable from the general mean, and significant differences from the null model are provided by χ^2 test statistics and p-values.

Results

V-formation flight and fixed parental leadership

We successfully tracked the spring migration of an entire goose family with high-resolution GPS-accelerometer devices
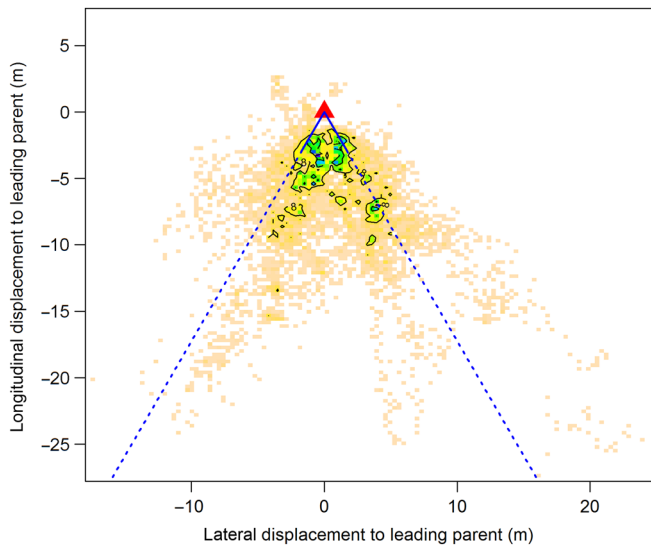
Figure 2. V-formation flight and parental leadership. Density plot with contour lines of relative positions of juveniles to the leading parent (at red triangle) aligned to move upwards. Blue lines indicate the median angle of juveniles toward the leading parent within the first 3 m; lines are extended as dotted lines for better visibility. See colour panel in Fig. 3.

(Fig. 1). We found that the family was organized in a clear V-formation (Fig. 2) that was maximally 39.8 m long (in flight direction) and 33.8 m wide, but 50% of all GPS points lay within an area of 5.1×5.2 m (length × width).

98.9% of all recorded chick locations had one or both parents in front of them (Fig. 2, 3), thus the formation was strongly aligned with respect to the leading parent. This was in 69.6% of the recordings the father, and in 29.3% cases the mother. Furthermore, in 59.7% of the cases both father and mother were in front of the chick(s) (Fig. 3).

No consistent flight mechanics differences of leadership but tail wind

Flapping frequency during flight, estimated by ODBA, differed between family members (status; i.e. mother, father and juveniles) and between leadership positions (i.e. leaders and followers) with an interaction between status and leadership position (GLMM, $\chi^2 = 43.44$, p < 0.001; Fig. 4a–b). Model estimates indicate that the father flapped less (−0.27) and the mother more than the juveniles (+0.04). The mother increased her flapping frequency slightly when she was leading the family (+0.06). The father, however, flapped less when he was in the lead (−0.09). All findings were confirmed by using wing beat frequency (Supplementary material Appendix 1 Fig. A3), thus highlighting the robustness of our findings.

The two tests of the relevance of body mass for the flapping frequency difference between father and mother showed that body mass was neither able to alone explain the patterns in ODBA (GLMM; $\chi^2 = 0.61$, p = 0.43; Fig. 4b), nor could its inclusion in the above model with status and leadership improve its explanatory power for the ODBA patterns

(GLMM; $\chi^2 = 1.62$, p = 0.20). Both parents reduced ODBA (and wing beat frequency, Supplementary material Appendix 1 Fig. A3), when experiencing supportive wind conditions (GLMM estimate −0.01, $\chi^2 = 84.41$, p < 0.001). But the father encountered stronger and more supportive winds when leading than the mother (GLMM estimate +1.31 m s^{-1}, $\chi^2 = 9.52$, p = 0.002; Fig. 3c).

Air speed was quadratically related to wind support for all family members with high air speed during head or strong tail winds (GLMM estimates +0.84 m s^{-1} + 0.10 m^2 s^{-2}, $\chi^2 = 25113$, p < 0.001, Supplementary material Appendix 1 Fig. A3). Thus, flight effort seems to be least at weak tail winds. Ground speed was positively related to wind support for all family members (GLMM estimate +1.50 m s^{-1}, $\chi^2 = 10964$, p < 0.001; Supplementary material Appendix 1 Fig. A3). Consequently, the goose family flew faster with tail winds and slower with head winds. The latter mainly happened during times when the mother was leading.

Discussion

We have analysed flight leadership and its consequences for flight mechanics of a complete family of wild white-fronted geese during their first spring migration. The family migrated in V-formation with one parent always leading. Although the father led the family group most of the time, he did not fly with higher flapping frequency while doing so. In contrast, the mother flapped more when leading, possibly because she experienced less supportive wind conditions when doing so. Air speed and ground speed were highly variable and related to tail wind, indicating that the geese were adapting their flight mechanics to possibly optimise flight effort and migration duration.

Nearly 100 percent of the recordings showed one parent in front of the family group. It has been argued that parents pay the additional energy cost of extended parental care (e.g. flying in front of the family group during migration), because of inclusive fitness advantages (Andersson and Wallander 2004). These benefits may even extend beyond migration, as cohesion of large families comes with increased dominance levels in foraging flocks (Black and Owen 1989) and parents may receive support with the subsequent brood from last-year juveniles (Ely 1993, Fox et al. 1995). Also, the father who mostly led the family did not pay a high price, because he flapped less, i.e. possibly spent less energy, when leading compared to following.

Adult male geese are generally larger than juveniles and adult females. Thus, the father might have experienced different wing loading enabling him to fly more easily. However, our tests could not confirm a direct relationship of flight mechanics to body mass. Still, flight mechanics of the different family members might have been differently affected by the extra weight and possible discomfort of carrying the neck ring and backpack transmitter. The father may have been affected less, because of larger body mass and more flight experience. But, as the geese were equipped with the tags over
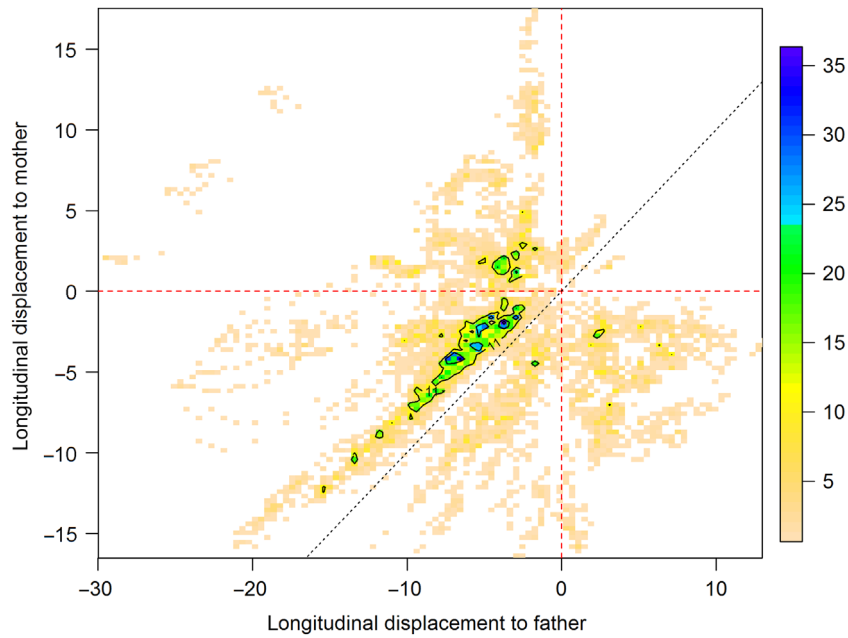
Figure 3. Juvenile positions to father and mother. Density plot with contour lines of longitudinal displacements of juveniles to father and mother, indicating that only at rare occasions a juvenile was flying ahead of one or both parents. Note that positive (negative) displacements indicate juveniles in front of (behind) the respective parent. The dotted black line indicates the unlikely positions with identical distance to father and mother. The high densities parallel to this line point out that also the parents aimed at staying close to each other.

four months before spring migration, we expect them to have habituated to the tags meanwhile.

A study on wild pelicans (Weimerskirch et al. 2001) showed that during short, low-level flights, individuals flying in front of a formation had a higher wing beat frequency than those following. This is opposite to our findings of complete migration flights over thousands of kilometres, where only the leading mother showed increased flapping frequency, but not the leading father. During spring migration, greater white-fronted geese are usually observed in large flocks (Polakowski et al. 2019), indicating that the family group was not migrating independently but integrated in a larger V-formation. Thus, the leading parent was likely following another (not GPS tagged) goose most of the time. Leadership would then only apply to the family group within, and have social components rather than energetic ones. So, it is possible that higher dominance levels of the male than of the smaller female have allowed him to fly in the region of upwash of an unrelated goose, whereas the female had to take a less favourable position.

In comparison, human-led migration of a single group of juvenile bald ibises showed that these birds regularly changed leadership (Voelkl et al. 2015, Voelkl and Fritz 2017). In this setup, however, the flock was not composed of all family members, but only of juveniles with similar flight ability, indicating that cooperation should mainly be established through reciprocity (Andersson and Wallander 2004, Voelkl et al. 2015). In addition, the migration of the juvenile bald ibis group was guided by humans in an ultralight aircraft, so that there was no need for transferring route information from parents to offspring.

In addition to cooperation based on kin selection, the V-formation may also improve the communication between individuals (Hamilton 1967, Gould and Heppner 1974). A constant angle between the individuals may aid social learning which is crucial for juvenile geese as they need to learn about the route, stopovers, dangers and optimal flight behaviour from their parents during their first spring migration. In groups of homing pigeons less experienced birds followed more experienced flock members, ultimately leading to enhanced route learning (Flack et al. 2012, Pettit et al. 2013, Sasaki and Biro 2017). Thus, the varying experiences of the different goose family members may have led to constant following of some group members, i.e. the juveniles.

We observed that the father and mother changed leadership depending on wind conditions. The father seems to have selected to lead during stronger tail winds and avoided to lead with head winds. This possibly explains the father's lower values of ODBA (and wing beat frequency) when leading. To let the female take the lead during weaker tail winds or during head winds might be due to exhaustion and necessary sharing of leadership in bad conditions. Furthermore, due to higher body mass the father may have been better able at handling strong tail winds than the mother, thus making him the better leader so that orientation is kept correctly at high ground speeds. In addition, the father might have been older and more experienced in wind use than the female.

We are confident that our sample size of GPS bursts and positions was sufficient to draw conclusions about flight leadership and flight mechanics consequences in the tracked family during spring migration. However, similar to the results drawn from a single group of bald ibises (Portugal et al.
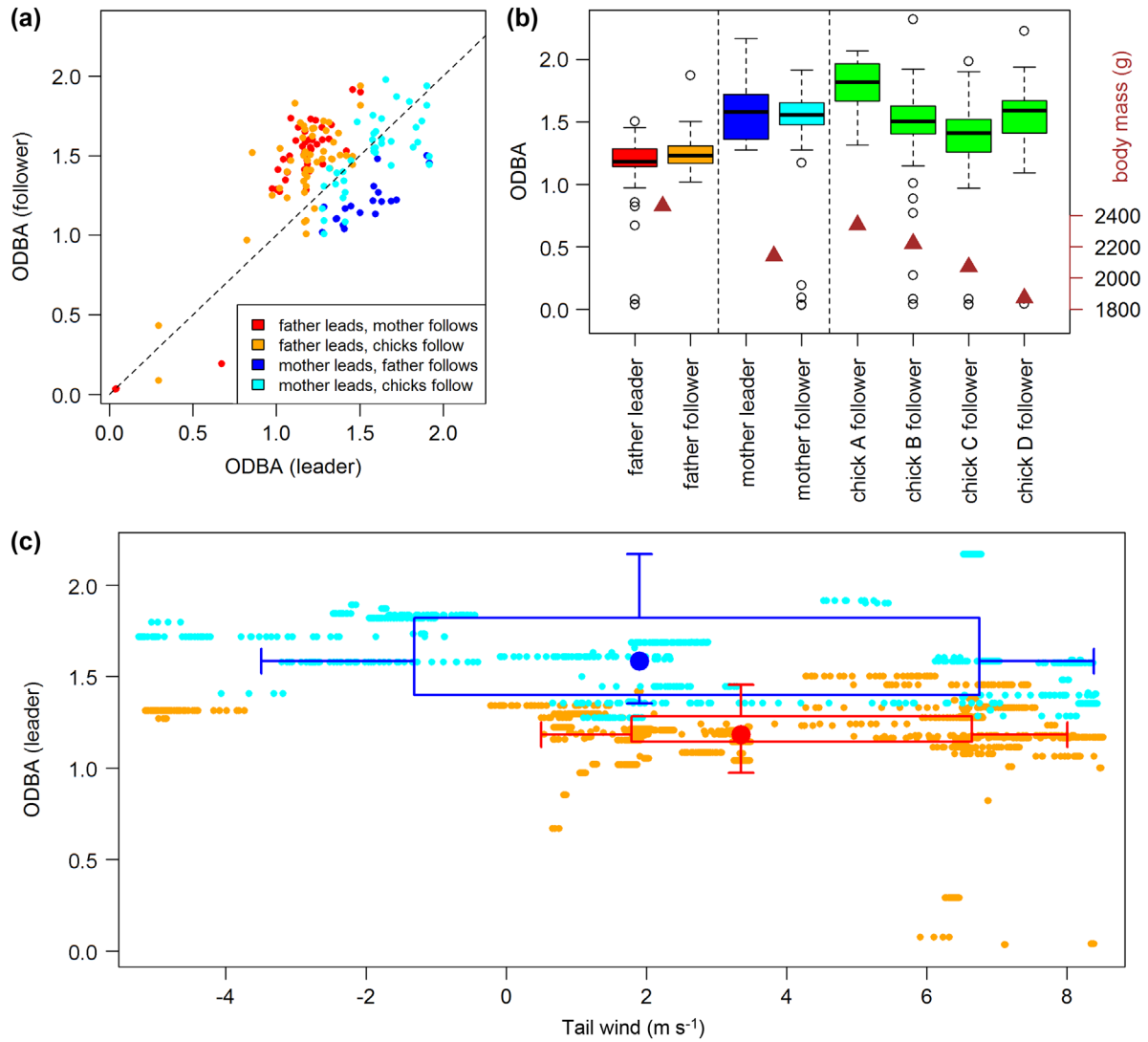
Figure 4. Flight mechanics influenced by leadership and wind. Overall dynamic body acceleration (ODBA) and tail wind experienced by the parental leader and direct follower (<3 m longitudinal displacement). (a) ODBA of leader versus follower indicating that the father had a lower flapping frequency when leading then the mother or following chicks. (b) Boxplots of ODBA compared between family members and their leadership rank. Brown triangles indicate body mass of the individual geese. (c) Tail wind for father (orange) and mother (light blue) when leading. Big dots indicate medians, boxes quantiles and whiskers 5% and 95% quartiles of both measures for father (red) and mother (blue), revealing that there was notably stronger tail wind when the father led the family group.

2014), we have data over the complete migration for only one family. This is mainly due to the difficulty of tracking entire families and the high mortality or tag failure during spring migration. Still, our data are obtained from different regions and times along the migration route, which allows for some spatial and temporal generalisation. Furthermore, we have spring migration tracking data of a second family (5 GPS bursts with 543 positions; Supplementary material Appendix 1 Fig. A5). Leadership patterns (Supplementary material Appendix 1 Fig. A5a; 79.4% father leads, 18.9% mother leads) and flapping frequency (Supplementary material Appendix 1 Fig. A6) agree with our findings presented here, indicating that our conclusions are generalizable to some extent.

We propose that for social migration in family groups, leadership is not shared equally to allow energy saving for all flock members. Instead, kin selection, experience and the need for juveniles to learn the different aspects important for successful migration may, in fact, shape leadership patterns. This might be generalizable to other socially flying animals, but likely only for species that move in groups or sub-groups of individuals with high heterogeneity in age, experience and flight ability. In the here observed goose family, the parents seemed to be the true leaders at all times, emphasizing the importance of kinship and social learning. To confirm learning, however, we would need to compare the juveniles' first year migration with that of the following spring. This would require collecting life time tracks of the juveniles, from which

one could obtain further insights in the variability of migration routes and timing, and how that could relate to recent high levels of climate and habitat change (Marra et al. 2005, Bauer et al. 2008).

Transparent Peer Review

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Data availability

Data available from Movebank Digital Repository: <doi: 10.5441/001/1.ms87s2m6> (Kölzsch et al. 2020).

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