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Original Article

Migration strategy of a flight generalist, the Lesser Black-backed Gull *Larus fuscus*

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Migrating birds are believed to minimize the time spent on migration rather than energy. Birds seem to maximize migration speed in different ways as a noteworthy variation in migration strategies exists. We studied migration strategies of a flight mode and feeding generalist, the Lesser Black-backed Gull *Larus fuscus*, using GPS-based satellite telemetry. We expected the gulls to achieve very high overall migration speeds by traveling via the shortest direct route, traveling during a large part of the day and night, and making few and short stopovers. Fourteen individuals were tracked between the Dutch breeding colony and the wintering sites in England, southern Europe and northwest Africa. The gulls did not travel via the shortest possible route but made substantial detours by their tendency to follow coasts. Although the gulls traveled during most of the day, and sometimes during the night, they did not achieve long daily distances (177 and 176 km/day in autumn and spring, respectively), which is explained by the gulls stopping frequently on travel days to forage. Furthermore, due to frequent and long migratory stopovers, their overall migration speed was among the lowest recorded for migratory birds (44 and 98 km/day, in autumn and spring, respectively). A possible explanation for the unexpected frequent stopovers and low migration speeds is that gulls do not minimize the duration of migration but rather minimize the costs of migration. Energy rather than time might be important for short-distance migrating birds, resulting in very different migration strategies compared with long-distance migrants. *Key words:* animal movement, currency, flight modes, migration strategies, migratory stopover. *[Behav Ecol 23:58–68 (2012)]*

INTRODUCTION

It is commonly believed that migrating birds minimize the duration of migration rather than the cost of migration (Alerstam and Lindström 1990; Hedenström 1993). A fast migration is thought to be beneficial because 1) migration is a dangerous undertaking (Strandberg et al. 2010), thus a faster migration reduces mortality risks; 2) migration generally takes a lot of time and in such a way "competes" with other activities within the annual cycle (Buehler and Piersma 2008), thus a faster migration creates leeway for molt and reproduction; and 3) early arrival is generally beneficial as it allows the individual to occupy better wintering and breeding territories (Kokko 1999; Norris et al. 2004). There seem to be very different ways by which different species minimize the duration of migration (i.e., maximize overall migration speed, the speed of migration including the time to accumulate the energy required for flight) as there is a noteworthy interspecific variation in migration strategies.

A lot of the variation in the behavior of migrants can be understood from their size and flight mode (cf. Hedenström 1993). Small birds minimize the duration of migration by traveling by self-powered flapping flight, whereas other factors determine whether they fly during the day, night, or both day and night (Alerstam 2009). For larger birds, thermal soaring flight is more profitable; flapping flight becomes less attractive because the energetic cost of flight increases; and mass-specific fueling rate declines with increasing body size (Åkesson and Hedenström 2007; but see Sapir et al. 2010). Thermals develop during the day and predominantly over land, and thus, soaring migration using thermals is restricted to daytime hours and to land (Kerlinger 1989). By far the highest overall migration speeds have been reported for seabirds that travel by dynamic soaring flight, such as albatrosses and shearwaters (Hedenström and Alerstam 1998; Åkesson and Hedenström 2007). This flight strategy, however, requires specific morphological adaptations, notably long and narrow wings (high aspect ratio wings).

Gulls (Laridae) are an interesting group in this respect as they are flight style generalists (Rayner 1988). During nonmigratory flights gulls often travel by flapping flight, especially at high flight speeds (Shamoun-Baranes and van Loon 2006). Gull wings have a relatively low wing loading (cf. Alerstam et al. 2007), allowing the birds to exploit thermals (thermal soaring flight) and updrafts that occur when winds hit an obstacle such as mountain ranges or coasts (ridge soaring, Kerlinger 1989). At the same time, gull wings have a relatively high aspect ratio, suitable for dynamic soaring flight. Gulls thus master a great variety of flight modes, although they are no true specialist in any particular flight style (Shamoun-Baranes and van Loon 2006). Furthermore, gulls are feeding generalists, that is, they can find food in almost any habitat. This means that suitable feeding habitat is available virtually everywhere along their migratory route,

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which is a rather uncommon situation for migrants. How this flexibility in flight modes and feeding habits subsequently affects migration strategies is unknown, mainly because gulls have hitherto received little attention in migration studies (but see Pütz et al. 2007, 2008). Ringing and especially color ringing has revealed some basic spatial aspects of gull migration, such as general migration routes and wintering areas (e.g., Baker 1980; Galván et al. 2003; Helberg et al. 2009; Kees (C. J.) Camphuysen, unpublished data), but we are still far from an understanding about how individual gulls exactly organize their migratory travels.

In this study, we explore the migration strategies of the Lesser Black-backed Gull *Larus fuscus*. We expect that these gulls are able to achieve very high overall migration speeds, for 4 main reasons. First, as the gulls master a variety of flight modes they are not restricted to travel over land or over water. The gulls thus do not have to make long detours related to general topography but could travel via the shortest direct route. A shorter migration distance will contribute to a high overall migration speed. Second, the flexibility in flight mode also implies that gulls are not restricted to travel during a certain time of the day, in contrast to, for example, thermal soaring migrants such as raptors for which traveling is limited to midday hours when atmospheric conditions are favorable. As gulls can travel many hours per day they could achieve relatively high daily travel speeds (distance covered on travel days), which will contribute to a high migration speed. Third, some of the possible flight modes are very energy efficient (notably thermal soaring, ridge soaring, and dynamic soaring flight). Low transportation costs would imply few and short stopovers to refuel and contribute to high migration speeds. Final, the abundance of food along the migration route will enable gulls to stop frequently to feed and thus allow them to travel relatively lean. Gulls could feed before and after daily flights and even interrupt flights whenever a good feeding opportunity occurs. The behavior to combine migration with foraging has been called fly-and-forage migration (Strandberg and Alerstam 2007; Klaassen et al. 2008). The general advantage of traveling lean is that the costs associated with carrying along fuel loads are avoided (Pennycuick 1989), saving energy and (stopover) time, resulting in high migration speeds.

More specifically we predict that 1) Lesser Black-backed Gulls generally travel via the shortest possible route (i.e., great circle routes, Imboden and Imboden 1972), not making detours related to topography. 2) The gulls use a wide daily time window for traveling and thus achieve relatively high daily travel speeds, exceeding the travel speeds of thermal soaring migrants. 3) Lesser Black-backed Gulls make few and short stopovers. 4) Lesser Black-backed Gulls achieve high overall migration speeds.

In order to test these predictions, we analyzed migratory movements of 14 Lesser Black-backed Gulls, as recorded by GPS-based satellite telemetry. We explore migratory routes, study stopover behavior and daily activity patterns, and determine daily travel rates and overall migration speeds. We also look into instantaneous flight speeds and altitudes of migration, to study flight behavior and thereby facilitate explaining observed patterns.

MATERIALS AND METHODS

Satellite tracking

Between 30 May and 12 June 2007, 14 adult Lesser Black-backed Gulls were caught on their nests in a large breeding colony in the Netherlands (Vliehors, Vlieland, 53.23°N–4.91°E) and fitted with solar powered Argos/GPS PTTs (PTT 100 series, Microwave Telemetry Inc., Columbia, MD). The satellite transmitters were attached as backpacks with a harness made of 2-mm-wide nylon string inserted in 7-mm-wide Teflon ribbon (Bally Ribbon Mills, Bally, PA). All birds were measured, weighed, sexed and (color) ringed, and released between 30 and 120 min after capture, depending on the number of birds caught at the same occasion.

Two types of Argos/GPS PTTs were used. Six birds were fitted with 22-g transmitters that only provide GPS locations (accuracy ± 18 m). The other 8 birds were fitted with 30-g transmitters that in addition provide details about the instantaneous ground speed (±1 km/h), altitude above mean sea level (±22 m), and instantaneous direction (±1°; all accuracy estimates according to the manufacture, Microwave Telemetry Inc.). Transmitters were programmed to obtain locations according to 1 of 5 possible schedules, differing in the start and end time, the interval between subsequent fixes, and thus in the number of fixes per day (see Supplementary Appendix 1). For the most intensive schedule, PTTs were programmed to take GPS fixes at an hourly basis between 5:00 and 22:00 (18 fixes/day). However, normally only about 8–10 fixes/day were actually obtained. At the least intense schedule, locations were logged every fourth hour, between 0:00 and 24:00 (6 fixes/day). Often 5–6 fixes were actually obtained on a day. For further details about duty cycles and the performance of the different transmitters, see Ens et al. (2009).

Bird FAFL stopped transmitting after it had reached its wintering area. All other birds were tracked until at least the next summer. Not all remaining birds carrying transmitters bred successfully summer 2008, but some of these bred successfully in subsequent years.

Analysis

Data from 31 May 2007 to 1 June 2008 were included, covering one autumn and one spring migration. The onset of autumn migration was defined as the last day, the bird was present at the breeding colony. Premigratory trips (see Results) are thus not included in the migration period. The end of the autumn migration was defined as the first day, the bird arrived at its first wintering site (some gulls used multiple sites during the winter, see Results). We assumed that sites visited during December–February are wintering sites. Spring migration was defined in an equivalent way: the onset of migration was the last day, the bird was present at (one of) the wintering site(s), the end of migration was the first day, the bird was back at the breeding colony (postmigratory trips are not included in the migration period).

During migration gulls typically used the same types of habitat to spend the night (buildings or lakes). A stopover day is defined by the bird using the same night roost as the previous night. In some cases, the birds alternated between 2-4 possible night roosts. Days on which the birds changed only night roost were not considered as travel days. A travel day is a day during which the bird changed the location where it roosted and made progress toward the goal (the minimum distance covered on a travel day was 25 km). The distance covered on a travel day is the rhumb line distance (Imboden and Imboden 1972) between subsequent night roosts. The total migration distance is the sum of the distances on travel days (excluding premigratory and postmigratory movements and excluding movements during the winter).

The instantaneous speeds and altitude above ground were analyzed for the 8 birds fitted with 30-g transmitters. For every position, the times of sunrise and sunset were computed using the NOAA-ESRL Sunrise/Sunset calculator (http://www.srrb.noaa.gov/), in order to evaluate whether the birds were traveling during the day or the night. Altitude above the ground was calculated by subtracting ground elevation from the bird's measured altitude above mean sea level. Ground elevations were obtained from the NASA Shuttle Radar Topographic Mission (SRTM) 90-m digital elevation data set (http://srtm.csi.cgiar.org/). When comparing instantaneous speeds with hourly flight speeds, we only included segments spanning 1 or 2 h.

RESULTS

Spatial patterns

All 14 Lesser Black-backed Gulls made successful migrations to wintering sites in Spain (9), Portugal (2), Morocco (1), France (1), and England (1) (Figure 1, Supplementary Appendix 1). One PTT stopped transmitting in southern Spain (October 2007), presumably after the gull had reached its wintering area. Spring tracks were thus obtained for 13 individuals. The great circle distance between the breeding colony and the wintering sites was on average 1672 km (Table 1). The gulls did not migrate along shortest possible routes but regularly made substantial detours (e.g., see individual MAFD in Figure 2). Consequently, the total migration distance was on average 21.1% and 17.9% longer than the shortest distance, for autumn and spring, respectively.

Prior to the autumn migration, half of the birds made a visit to a distant site after which they returned to the breeding colony (Figure 2, Supplementary Appendix 1). These movements differed from foraging trips during the breeding season in both distance and duration (Supplementary Appendix 2). We called these trips premigratory movements. Two birds even made 2 such movements within 1 season. During the autumn migration, 5 of 7 birds returned to the site that was visited during the premigratory movement and made a stopover at this location (e.g., individual MAFD in Figure 2). Also after the spring migration, about half of the gulls made very similar round trips to distant sites, named postmigratory movements (Figure 2, Supplementary Appendix 1 and 2).

The Lesser Black-backed Gulls regularly migrated over land, over water as well as along coasts (Figures 1 and 2). Travels over land were sometimes necessary to reach inland stopover and wintering sites but also, for example, Brittany (France) was crossed over land rather than making a detour along the coast (Figures 1 and 2). Long sea crossings up to 700 km were made between England and France and over the Bay of Biscay. No consistency could be detected in whether individual birds would cross the sea or travel along the coast. For example, individual MAFR made a direct sea crossing of the Bay of Biscay in the autumn, whereas in the spring, it followed the Spanish/French coast (Figure 2).

Temporal patterns

The gulls departed on their autumn migration between 21 June and 5 August. There was more spread in the arrival date at the wintering grounds; the birds completed autumn migration between 22 July and 22 December (Figure 3). There was less spread again in the departure and arrival dates in spring (Figure 3). There was a tendency that individuals which departed early in autumn arrived late at their wintering site. This effect was, however, not significant ($r = -0.51$, $P = 0.06$, $n = 14$). Neither could we show any carryover effect; birds that arrived late at their wintering site did not leave later in

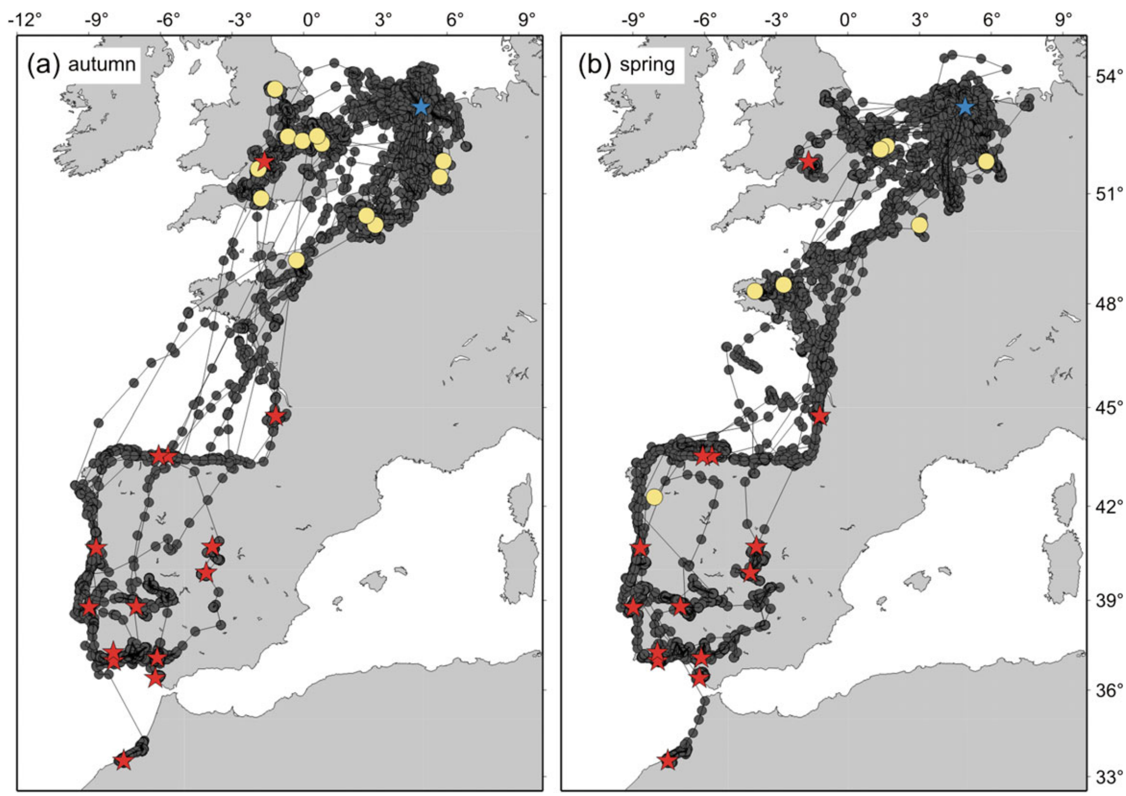

Figure 1
General overview of movements of Lesser Black-backed Gulls as tracked by GPS-based satellite telemetry in autumn (a) and spring (b). (a) GPS positions from 14 individual birds obtained between 1 June and 31 December 2007. (b) GPS positions from 13 individual birds obtained between 1 January and 31 May 2008. The location of the breeding colony is indicated by a blue star, wintering sites by red stars, and important stopover sites (see Supplementary Appendix 1) by yellow circles.

Table 1
Distances and temporal aspects of autumn and spring migration, for 14 Lesser Black-backed Gulls tracked by satellite telemetry

	Autumn migration Average (Range)	Spring migration Average (Range)
Onset of migration	14 Jul (21 Jun–5 Aug)	25 Mar (1 Mar–13 Apr)
Arrival at wintering ground	5 Oct (22 Jul–22 Dec)	16 Apr (30 Mar–19 May)
Duration of migration (days)	83.0 (8–175)	22.9 (6–43)
Number of travel days	12.4 (5–26)	11.5 (3–18)
Total migration distance (km)	2036 (622–2641)	1965 (486–2898)
Travel speed (km/day)	177.1 (101.6–265.9)	175.8 (105.4–293.4)
Migration speed (km/day)	44.2 (10.3–152.5)	97.7 (42.5–192.8)
Direct distance (km)	1672 (473–2059)	

Migration speed is the overall migration speed, including stopover time. Travel speed is calculated as the average distance covered per day on travel days only. The direct distance is the length of the great circle route between the breeding colony and the (first) wintering area. The full table, with data for each individual bird, is available in Supplementary Appendix 3.

the following spring ($r = -0.42$, $P = 0.17$, $n = 13$). Only the correlation between the onset of spring migration and the arrival at the breeding site was significant ($r = 0.67$, $P = 0.01$, $n = 13$). No correlations were detected between the timing of migration and the distance to the wintering site. Thus, birds that wintered further away from the breeding colony did not depart earlier from the breeding colony in autumn nor arrive later at their wintering site in autumn. Furthermore, they did not depart earlier from the wintering site in spring nor arrive later at the breeding colony in spring ($P > 0.05$ for all correlations tested).

Both in autumn and in spring, the majority of gulls did not travel continuously but alternated between travel and stopover days (Figure 3); only 2 trips were without a stopover (MAFP in

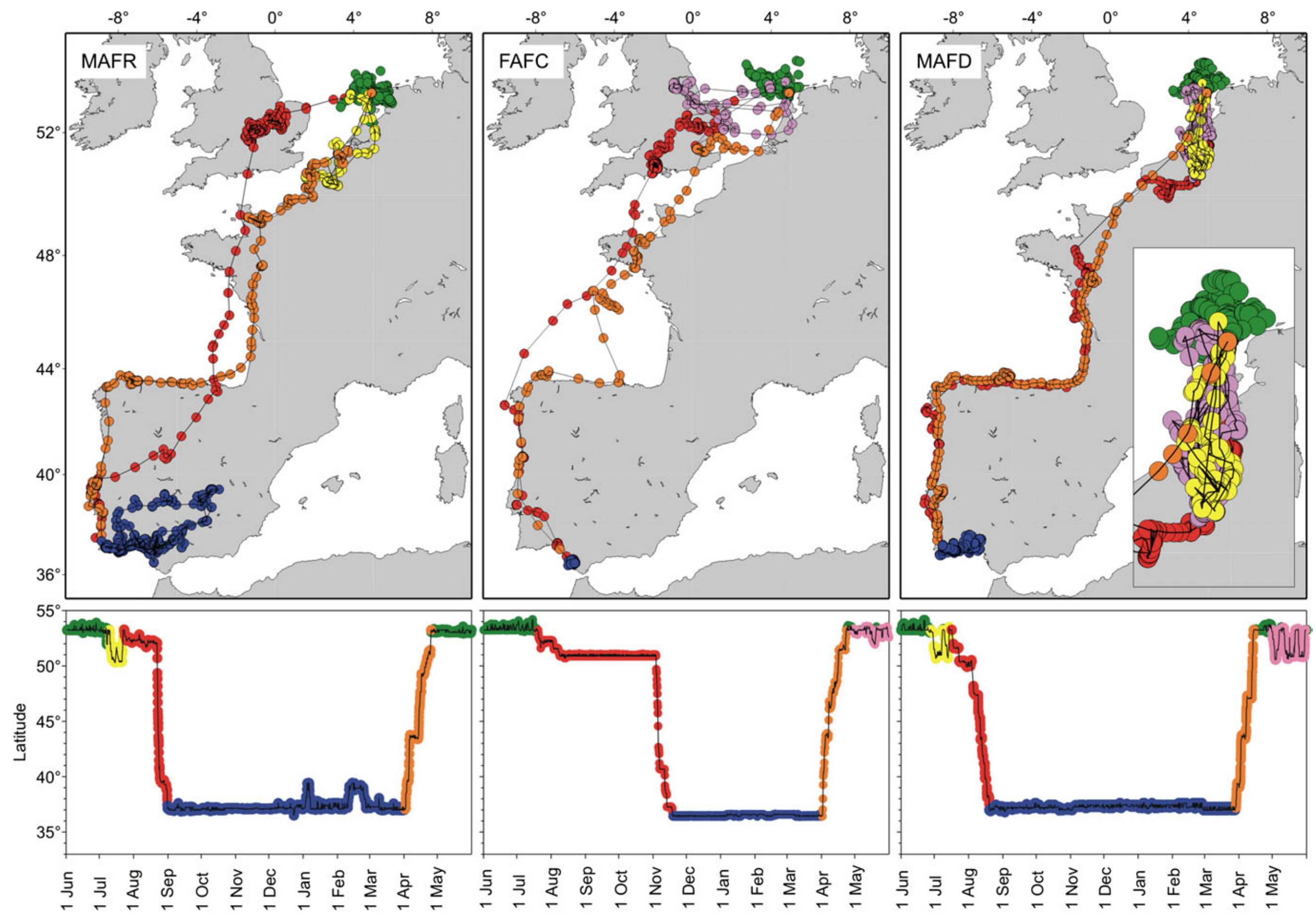

Figure 2
Three representative migratory travels of Lesser Black-backed Gulls illustrating premigratory and postmigratory movements (see also Supplementary Appendix 4). Lower panels depict latitude over time. We distinguished between breeding season (green), premigratory loops (yellow), autumn migration (red), wintering area (blue), spring migration (orange), and postmigratory loops (pink). Bird MAFR made an excursion during the winter.

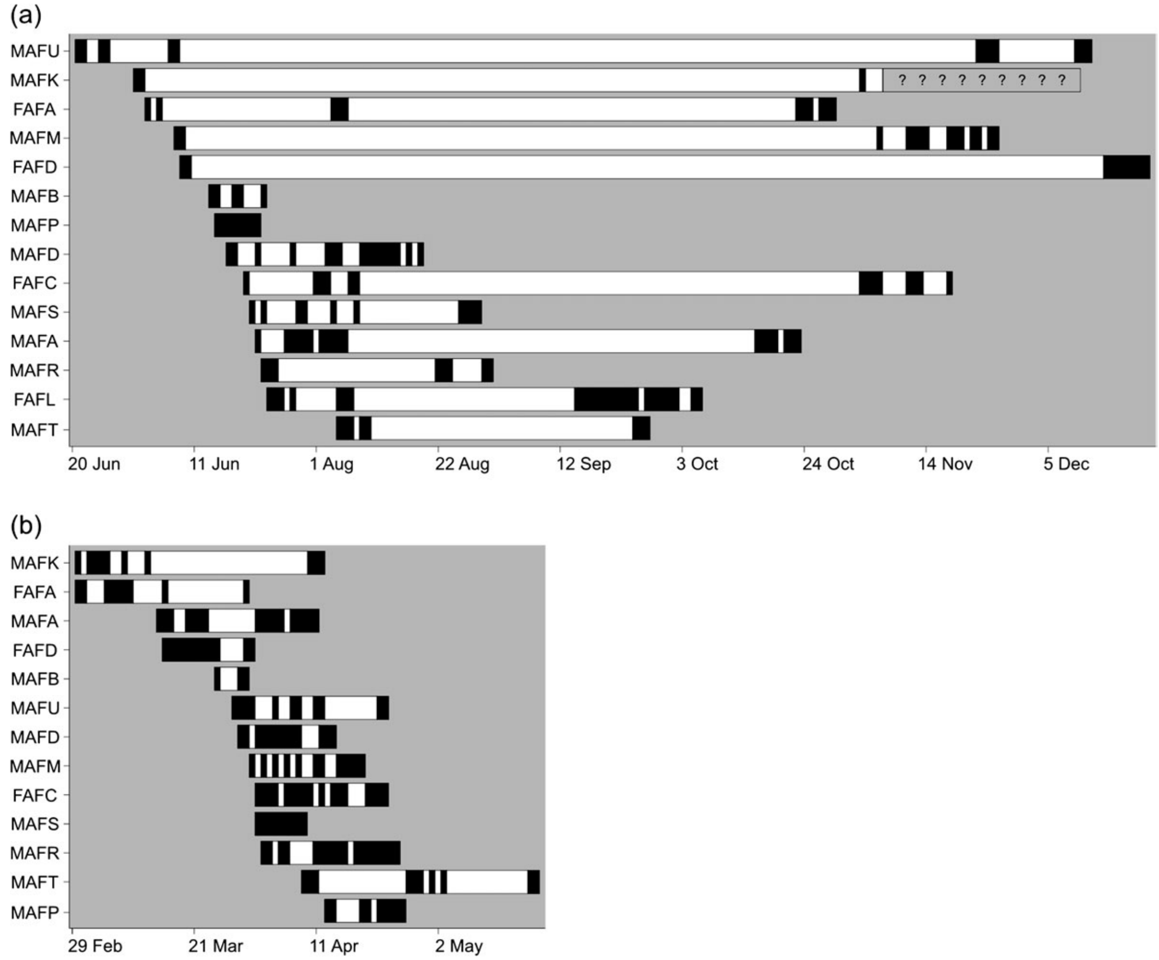

Figure 3
Travel and stopover days during autumn (a) and spring migration (b) of individual birds. For every day, it was classified whether the bird made a migratory movement (travel day, in black) or not (stopover day, in white). The minimum distance covered on a travel day was 25 km. Commuting movements between feeding and resting sites within a stopover site were not regarded as migratory movements and classified as part of stopover day(s). For individual MAFK, no data were obtained during the last weeks of its autumn migration. Individual FAFL was not tracked during spring. Birds were ranked after departure date.

autumn, MAFS in spring). There was an enormous variation in the number and duration of stopovers. In the autumn, birds made on average 3.4 stopovers (range 0–6), and the average duration of a stopover was 22.2 days (range 1–157 days). In total, 11 of 14 birds made noticeable long stopovers (>14 days), ranging from 17 to 157 days (on average 77 days, Supplementary Appendix 1). All these longer stopovers were made in northern Europe, relatively close to the breeding colony (Figure 1). In the spring, the birds made slightly fewer stopovers (on average 2.8 per bird, range 0–6), and the duration of a stopover was much shorter (average 4.0 days, range 1–27 days; pairwise t-test: $t_{11} = 3.8$, $P = 0.002$). In spring, only 2 birds made stopovers > 14 days (Supplementary Appendix 1, Figure 3). There was no difference in the number of travel days between the seasons (on average 12.4 and 11.5 days for autumn and spring, respectively; pairwise t-test: $t_{11} = 0.4$, $P = 0.7$). Overall, the autumn migration took much longer than the spring migration (83 vs. 23 days, Table 1; pairwise t-test: $t_{12} = 4.2$, $P = 0.001$). This is also reflected in the overall migration speed, which is much lower in autumn (44 km/day) than in spring (98 km/day, Table 1; pairwise t-test: $t_{12} = -3.6$, $P = 0.004$). However, the speed on travel days was comparable between autumn and spring (177 and 176 km/day, respectively, Table 1; pairwise t-test: $t_{12} = 0.63$, $P = 0.54$).

Instantaneous speeds and altitudes

Instantaneous speeds and altitudes could only be evaluated for the 8 birds carrying 30-g transmitters. On travel days, the average instantaneous speed as recorded in this study was 38.6 km/h (excluding instantaneous speeds < 10 km/h which will predominantly include occasions of sitting, walking, or birds floating on water (Shamoun-Baranes et al. 2011), although inclusion of a few occasions of soaring flight cannot completely be excluded, cf. Shamoun-Baranes and van Loon 2006). Movements with instantaneous speeds > 10 km/h occurred predominantly during daytime (Figure 4). Movements during the night were relatively rare and mainly occurred on days when the birds covered relatively large daily distances (Figure 4). The total distance covered during a day was positively correlated with the average instantaneous flight speed (average for locations with instantaneous speeds > 10 km/h, $r = 0.33$, $P < 0.001$). Interestingly, instantaneous speeds were higher than hourly travel speeds, as derived from subsequent GPS fixes (Figure 5; pairwise t-test: $t_{1201} = 17.7$, $P < 0.001$). The mean hourly travel speed was 23.5 km/h.

On travel days, the gulls only very rarely flew higher than 250 m above the ground, both in autumn and in spring (Figure 6). The maximum altitude above the ground as recorded in this

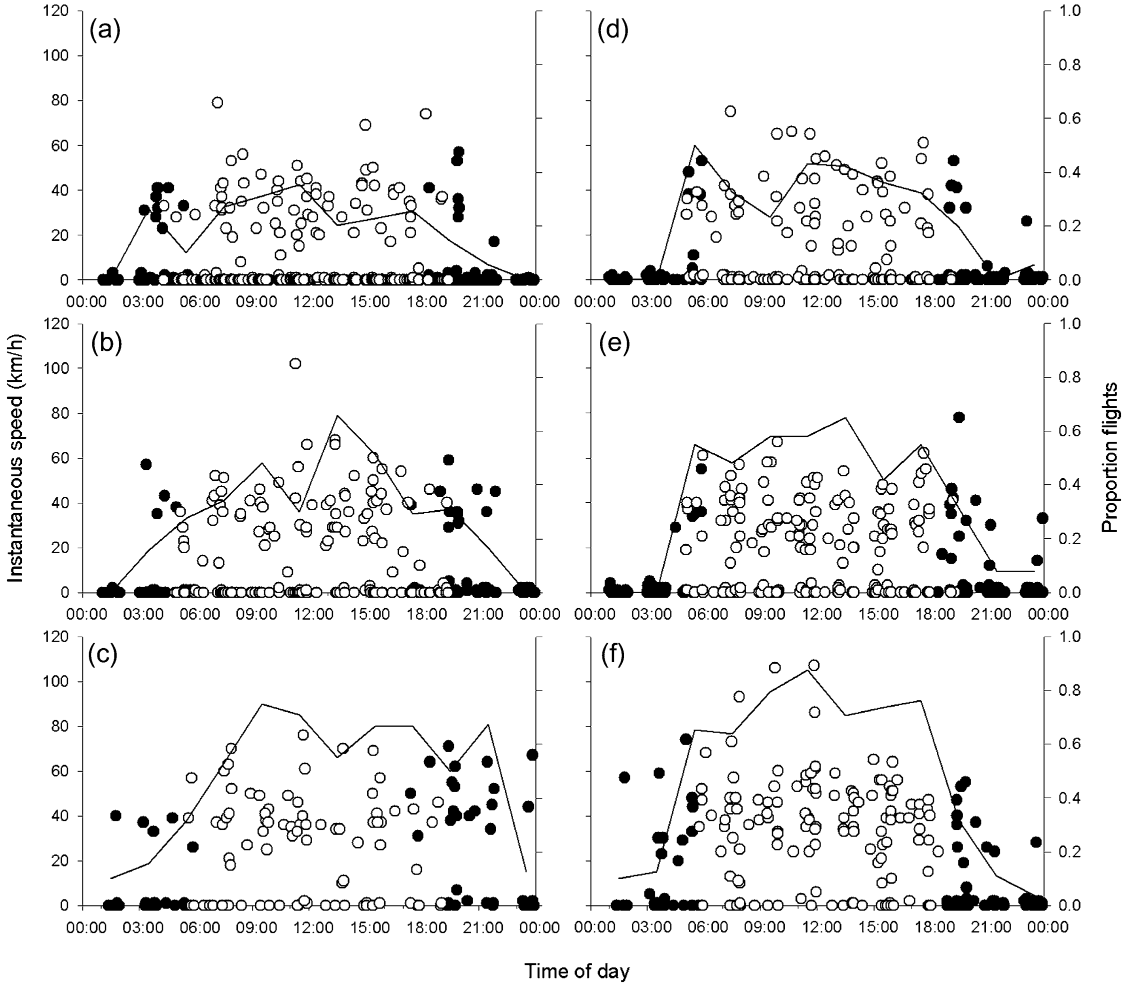

Figure 4
Activity patterns of 8 Lesser Black-backed Gulls on travel days. Instantaneous speeds (km/h, left *y* axis), as recorded by GPS-based satellite telemetry, are shown in relation to local time of day. White and black dots indicate registrations during daylight and darkness, respectively. Note that there can be overlap in daylight and darkness registrations as the times of sunrise and sunset depend on location and time of year. Lines depict the proportion of flights, that is, the proportion of fixes per 2 h intervals with instantaneous speeds > 10 km/h; right *y* axis. Daily activity patterns are summarized for autumn (a–c) and spring (d–f) and for days at which a relatively short (<75 km, a and d), intermediate (75–200 km, b and e), and long (>200 km, c and f) travel distance.

study was 1744 m. Negative values predominantly arose from errors in the ground elevation model, especially in areas with a heterogeneous topography.

DISCUSSION

General routes

Different individuals followed very different routes, made stopovers at different localities, and wintered in different areas, despite the fact that these birds were tagged at the same breeding colony. This diversity in routes is in contrast to many species of waterfowl that tend to congregate at a few important stopover sites (e.g., Brent Goose *Branta bernicla*—Green et al. 2002; Bewick's Swan *Cygnus columbianus*—Beekman et al. 2002) and for some soaring migrants that are strongly guided by topography (e.g., Swainson's Hawk *Buteo swainsoni*—Fuller et al. 1998; White Stork *Ciconia ciconia*—Shamoun-Baranes et al. 2003). Migration routes even differed within individuals between seasons and seemingly more so than, for example, Ospreys *Pandion haliaetus* (Alerstam et al. 2006) and Marsh Harriers *Circus aeruginosus* (Vardanis et al. 2011).

We reasoned that Lesser Black-backed Gulls would not be guided by topography to the same extent as, for example, thermal soaring migrants who avoid traveling over water (Fuller et al. 1998; Hake et al. 2003; Bildstein and Zalles 2005), as gulls, being flight mode generalists, would not be restricted to travel over land or over water. We expected that gulls would thus travel along approximately the shortest routes between breeding and wintering sites. The gulls tracked in this study traveled over land as well as over water (sea). However, they did not travel along the shortest possible routes, migration routes were about 20% longer than great circle routes. This difference is substantial and similar to that noted for some thermal soaring birds circumventing the Mediterranean Sea (Leshem and Yom-Tov 1996), whereas, for example, migration routes of Marsh Harriers were only about 3% longer than shortest possible routes (Klaassen et al. 2010). The Lesser Black-backed Gulls made considerable detours, which seem to be the result of the tendency of the gulls to follow coasts. Gulls presumably follow coasts as this provides opportunities for ridge soaring and thus to travel with low energetic costs (see also below). Another possible reason for following coasts could be that coastal habitats provide plentiful feeding

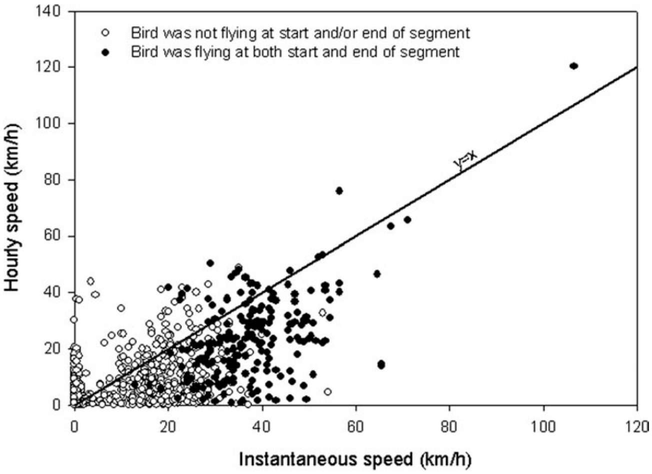

Figure 5
Instantaneous speed versus hourly flight speeds on travel days. Data for 8 birds included (autumn and spring travels combined). Segments are defined by subsequent GPS fixes. Segments with time intervals > 2 h were excluded. Hourly speeds are the distances between subsequent GPS fixes divided by the time interval. Instantaneous speed is the average for the instantaneous speed at the start and the end of the segment (i.e., the average of the 2 points used to calculate hourly speed). The solid line is the relationship $y = x$.

opportunities for gulls. Although gulls can also find food at sea and on land, coastal habitats presumably provide the most predictable food source.

Nonmigratory movements

The Lesser Black-backed Gulls turned out to be very mobile. During the breeding season, they mostly had a pelagic life, with almost daily fishing trips over the North Sea (with the exception of one individual that foraged exclusively on the mainland), up to 180 km from the nest (Ens et al. 2009). Autumn migrations were in half of the cases preceded by round trips to relatively distant locations, including the UK for example. The function of these premigratory movements is unknown, but they possibly have some exploratory character (prospecting). The gulls often (but not always) returned to the sites visited during their premigratory movements, either during autumn migration (e.g., individual MAFD, Figure 2) or during spring migration (e.g., individual MAFR). Also during the winter and after the spring migration, the gulls made long round trips, lasting several days. As the gulls were not breeding at these times, these trips could again be assumed to have some exploratory character. Exploratory round trips before or after the migratory travels and during the winter are uncommon in migrating birds, but they have, for example, been reported for Marsh Harriers (Strandberg et al. 2008). The fact that Lesser Black-backed Gulls make extensive foraging trips during the breeding season and lengthy round trips before autumn migration and after spring migration suggests that their travel costs are relatively low.

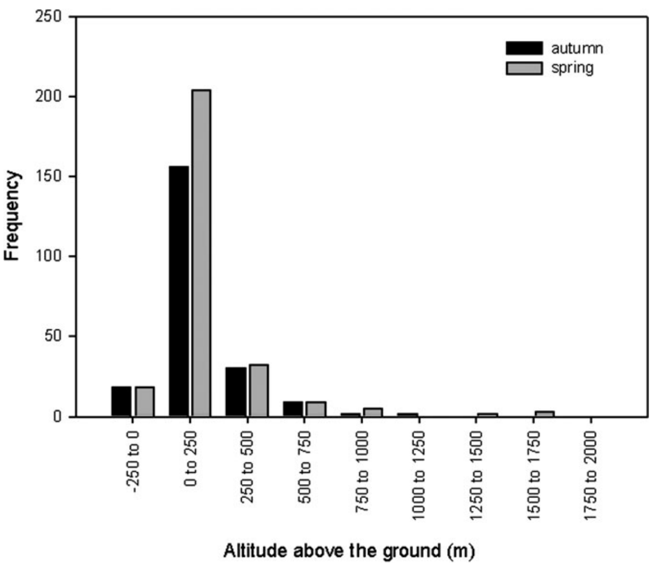

Figure 6
Altitudes of Lesser Black-backed Gulls on travel days, for locations with instantaneous speeds > 10 km/h (i.e., the bird is flying), for autumn and spring migration. Data for 8 birds included. Bird altitudes were obtained from GPS-based satellite telemetry; ground elevations were obtained from the NASA Shuttle Radar Topographic Mission 90-m digital elevation model (for details, see text).

Flight modes

A notable discrepancy exists between instantaneous speed (as recorded by the GPS transmitters) and hourly travel speed (as derived from subsequent GPS fixes), with instantaneous speeds being higher than hourly travel speeds (Figure 5). Such discrepancy is typical for birds traveling by thermal soaring or dynamic soaring flight as the ground track for a bird traveling by soaring flight is not a straight line as the birds are flying in circles (thermal soaring flight) or alternate between flying with the wind and against the wind (dynamic soaring flight). Also for ridge soaring, higher instantaneous speeds than ground speeds were recorded, although the difference seems less pronounced than for thermal and dynamic soaring flight (Kerlinger 1989). For flapping flight, we expect very little difference between instantaneous and hourly speeds (given that the bird travels in a straight line). An alternative explanation for the observed difference between instantaneous and hourly speeds is that the birds are regularly interrupting their flights, for example, in order to feed (fly-and-forage migration, see below). This might have happened on some days, when periods of flight alternated with periods of nonflight. However, on many other days, the birds seem to fly continuously, that is, for a series of subsequent location fixes the GPS indicated that the birds were flying. For segments, where the instantaneous speed > 0 km/h at both the start and the end of the segment, there was still a large discrepancy between instantaneous and hourly speeds, which is most likely to be the result of a soaring or mixed flight mode. Still, we cannot completely exclude that the gulls made short stops, as we only get positions every hour (in the best case). More detailed tracks (i.e., tracks with a much higher frequency of fixes) are needed to establish the relative importance of flight modes and fly-and-forage behavior on the resulting hourly flight speeds (Shamoun-Baranes et al. 2011).

Flight altitudes might provide further insight in the flight behavior of gulls. The great majority of the movements of the gulls tracked in this study occurred below 250 m above the ground (93%) and flights above 500 m were rare. Shamoun-Baranes and van Loon (2006) and Shamoun-Baranes et al. (2006) studied Lesser Black-backed Gulls during nonmigratory flights and reported that gulls travel at altitudes of about 175 and 300 m during flapping and soaring flight, respectively. Ospreys and Marsh Harriers, which travel often by thermal soaring flight, especially around midday, mainly fly between 100 and 750 m above the ground (RHG

Klaassen, unpublished data from GPS satellite tracking), and other soaring migrants reach even higher altitudes (Leshem and Yom-Tov 1996; Shannon et al. 2002; Shamoun-Baranes et al. 2003). Final, Schmaljohan et al. (2008) detected flocks of migrating Lesser Black-backed Gulls at very high altitudes (3500 m asl) during radar studies in the Sahara Desert. These birds were traveling by flapping and gliding flight. They were thought to occur at these high altitudes in order to exploit strong tailwinds. Although the altitudes at which the gulls were flying in this study do not provide a clear insight in the exact flight mode of the gulls, this information is still valuable as the range of altitudes used by the gulls does not exclude any mode of traveling. Clearly, the exact flight strategies of gulls during migration and differences with, for example, soaring migrants, remains to be established.

Travel and migration speeds

The gulls traveled during the day as well as during the night, although movements during the night were rare (only 8% of all recorded movements occurred in darkness). As expected, gulls nevertheless used a much wider time window for traveling than typical thermal soaring migrants such as raptors (Kerlinger 1989; Leshem and Yom-Tov 1996; Klaassen et al. 2008) and storks (Leshem and Yom-Tov 1996; Berthold et al. 2001). However, their daily travel distances were in fact somewhat shorter than for most soaring migrants (see Table 2). This discrepancy is most likely explained by the gulls devoting a substantial amount of time on travel days to foraging (i.e., fly-and-forage strategy). If we compare the daily travel speeds of the gulls with those for another fly-and-forage migrant, the Osprey (Klaassen et al. 2008), we see that the gulls achieved in fact slightly longer daily distances than the Osprey (176 vs. 142 km/day, respectively), supporting the idea that gulls can travel longer daily distances than raptors by traveling more hours per day.

Unexpectedly, the Lesser Black-backed Gulls regularly made stopovers, both in autumn and in spring. Gulls interrupted their migrations relatively often in comparison to, for example, thermal soaring migrants (Berthold et al. 2001; Alerstam et al. 2006) and waterfowl (Beekman et al. 2002; Green et al. 2002). In the autumn, most individuals made a relatively long stopover (>14 days) in northern Europe, lasting on average 77 days. The long duration of these stopovers suggest that they have another function than (only) accumulating fuel for the consecutive migratory flight, for example, flight feather molt. Lesser Black-backed Gulls already start their primary molt at the breeding site, but this is completed at the wintering site (Cramp 1983). Also the spring migration was regularly interrupted for stopovers, although spring stopovers were much shorter than autumn stopovers and long stopovers (>14 days) were rare in spring.

Due to the frequent and long stopovers, the resulting overall migration speed of Lesser Black-backed Gulls is strikingly low, both for autumn (44 km/day) and for spring (98 km/day) migration, and much lower than values reported for most thermal soaring migrants and dynamic soaring migrants (Table 2). This is very surprising as we had expected the gulls to be able to achieve very high migration speeds instead. The seasonal difference in migration speed is explained by a difference in the duration of migration. Autumn migration took on average 60 days longer than spring migration, which can be fully attributed to a difference in the number of stopover days (there was no seasonal difference in daily travel speeds, Table 1).

An energy minimizing migration strategy?

Migrating Lesser Black-backed Gulls behaved very differently from what we expected for a feeding generalist that masters a great variety of flight modes. Possibly the most unexpected finding is that the Lesser Black-backed Gulls made many and long stopovers, resulting in very low overall migration speeds. To some extent, we can explain this by assuming that these stopovers serve another function than refueling, but this seems only to be valid for the very long stopover in autumn. The fact that the gulls make many stopovers is especially striking as they seem to have low transportation costs and use a fly-and-forage migration strategy (i.e., they can almost instantaneously balance flight costs by finding food quickly), 2 factors that actually reduce the need for refueling stopovers.

So why are Lesser Black-backed Gulls migrating so slowly? A possible explanation could be that gulls do not have a time selective but rather an energy selective strategy (Hedenström 1993), that is, possibly the gulls do not minimize the duration of migration but rather the costs of migration. Strandberg et al. (2009) compared the duration and distance of migration of several species of birds of prey and conclude that a shift occurs in the balance between speed and duration of migration depending on migration distance. Migrants can save energy by traveling only under the most favorable weather conditions (tailwinds, strong thermals, etc.). However, such energy saving comes at the cost of a longer duration of migration (and hence lower overall migration speed) because the birds often have to wait for favorable conditions. Long-distance migrants presumably cannot afford to be very selective for weather conditions simply because this would make the duration of migration too long. In agreement with these ideas, it was observed that Common Buzzards *Buteo buteo* (a short-distance migrant) are indeed more selective for favorable weather than Honey Buzzards *Pernis apivorus* (a long-distance migrant) (Alerstam 1978). Furthermore, Ospreys (a long-distance migrant) are not selective for favorable weather (both precipitation and wind) (Thorup et al. 2006). Thus, the Lesser Black-backed Gulls, being short to intermediate distance migrants, could be saving energy by waiting for more favorable weather conditions, hence their frequent stops and thus slow migrations.

Another reason why gulls might not be "in a hurry," especially in the autumn, is that gulls do not defend territories at their wintering quarters (gulls are gregarious during the winter), that is, late arrival possibly does not come at a direct cost.

Conclusions and prospects

Lesser Black-backed Gulls seem to have a rather unique migration strategy among birds, with great variation in routes between and within individuals, flexible travel behavior (flying over land as well as over water, during the day and during the night), short daily distances and frequent stopovers, and an overall slow migration speed. These results are best explained by the gulls having an energy minimizing strategy, making them an exception to the rule that migrating birds maximize migration speeds.

GPS-based satellite telemetry has revealed the general migration strategies of Lesser Black-backed Gulls in great detail. Additional information on the instantaneous speed and altitude was particularly valuable to look at more detailed behaviors and time budgets. Nonetheless, it would be interesting to track the gulls in even greater detail, that is, a much higher frequency of fixes along with acceleration data to provide information on wing beat frequencies (e.g., Ropert-Coudert et al. 2004; Weimerskirch et al. 2005; Shamoun-Baranes et al. 2011), in order to be able to determine the flight modes of the gulls during different parts of their travels.

Final, it would also be very interesting to make comparisons with the eastern subspecies *L. fuscus fuscus*, which makes much longer migrations to wintering areas in east Africa south of the Sahara desert. Do these birds also "take it easy" despite a longer migration distance and the crossing of an ecological barrier?

Table 2

Travel and migration rates for a selection of well-studied species, for autumn (migration away from the breeding area) and spring (migration toward the breeding area) migration

Species	Flapping flight	Thermal soaring	Dynamic soaring	Distance (km)	Daily travel speed (km/day)		Overall migration speed (km/day)		References
					Autumn	Spring	Autumn	Spring	
Lesser Black-backed Gull *Larus fuscus*	x	x	x	2000	177	175	44	98	This study
A. Raptors									
Common Buzzard *Buteo buteo*		x		700	84	—	57	104	Strandberg et al. (2009)
Osprey *Pandion haliaetus*	(x)	x		6350	261	286	183	239	Alerstam et al. (2006)
Peregrine Falcon *Falco peregrinus*	x	x		8500	—	—	172	198	Fuller et al. (1998)
B. Herons, storks, cranes									
White-naped Crane *Grus vipio*	x	x		2550	~670	—	68[a]	—	Higuchi et al. (2004)
Purple Heron *Ardea purpurea*	x			4250	700	—	~66[a]	—	van der Winden et al. (2010)
White Stork *Ciconia ciconia*		x		5750	262	214	240	154	Shamoun-Baranes et al. (2003)/van den Bossche et al. (2002)
C. Waterfowl									
White-fronted Goose *Anser albifrons*	x			3000	—	670	—	~40[a]	Fox et al. (2003)
Bewick's Swan *Cygnus columbianus*	x			3200	757	303	44–72[a]	29–38[a]	Beekman et al. (2002)
Brent Goose *Branta bernicla*	x			5000	—	763	—	62[a]	Green et al. (2002)
D. Shorebirds									
Bar-tailed Godwit *Limosa lapponica*	x			10 150	1305	—	—	—	Gill et al. (2009)
Turnstone *Arenaria interpres*[b]	x			12 500	—	1000	—	360	Minton et al. (2010)
E. (near) Passerines									
Wood Thrush *Hylocichla mustelina*	x			3100	—	—	62	242	Stutchbury et al. (2009)
Hoopoe *Upupa epops*	x			3700	—	—	100	143	Bächler et al. (2010)
Purple Martin *Progne subis*	x			7150	500	—	153	429	Stutchbury et al. (2009)
F. Seabirds									
Albatrosses *Diomedia* sp.[c]			x	4200			356–552		Waugh and Weimerskirch (2003)
Sooty Shearwater *Puffinus griseus*			x		—	—	536–910	837	Shaffer et al. (2006)
Arctic Tern *Sterna paradisaea*	x		(x)	30 150	—	—	330	520	Egevang et al. (2010)

Daily travel speed is the average distance covered on travel days only. Overall migration speed is the speed including the time to fuel for flights, that is, including stopovers.

[a] Fueling time before departure is included.

[b] Birds were not tracked all the way; last part of spring migration is missing.

[c] These are long foraging movements rather than migratory movements.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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