



Original Article

Resource predictability drives interannual variation in migratory behavior in a long-lived bird

Jan M. Baert^{a,b,*,*}, Eric W.M. Stienen^c, Frederick Verbruggen^{d,*,*}, Nico Van de Weghe^e, Luc Lens^{b,*,*}, and Wendt Müller^{a,*,*}

^aDepartment of Biology, Behavioural Ecology and Ecophysiology Group, University of Antwerp, Universiteitsplein 1, 2610 Antwerp, Belgium, ^bDepartment of Biology, Terrestrial Ecology Unit, Ghent University, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium, ^cResearch Institute for Nature and Forest (INBO), Havenlaan 88 bus 73, 1000 Brussels, Belgium, ^dDepartment of Experimental Psychology, Ghent University, Henri Dunantlaan 22, 9000 Ghent, Belgium, and ^eDepartment of Geography, CartoGIS Unit, Ghent University, Krijgslaan 281, 9000 Ghent, Belgium

Received 7 May 2021; revised 15 October 2021; editorial decision 19 October 2021; accepted 27 October 2021; Advance Access publication 30 November 2021.

There is a growing awareness that experience may play a major role in migratory decisions, especially in long-lived species. However, empirical support remains to date scarce. Here, we use multiyear GPS-tracking data on 28 adult Lesser Black-backed Gulls (*Larus fuscus*), a long-lived species for which migratory strategies typically consist of a series of long stopovers, to assess how experience affects interannual variation in stopover selection. We expect that food source reliability should play a pivotal role, as it both reduces the uncertainty on food availability across years, and enables for more efficient foraging during stopovers by reducing searching efforts. We found that during stopovers gulls indeed developed high fidelity to particular foraging locations, which strongly reduced the daily distance travelled for foraging. When revisiting stopovers in consecutive years, birds used over 80% of foraging locations from the previous year. Although the average fidelity to stopovers across years was as high as 85%, stopovers where birds showed high foraging site fidelity were up to 60% more likely to be revisited compared to stopover with low foraging site fidelity. Accordingly, birds using more stopovers with reliable foraging opportunities showed significantly less interannual variation in their stopover use than birds using stopovers with less reliable foraging opportunities. Our results thus highlight the need to further deepen our understanding of the role of cognitive processes in individual variation in migratory behavior.

Key words: learning, Lesser Black-backed Gull, migration, selection, stopover.

INTRODUCTION

Many bird species undertake seasonal migrations to exploit spatiotemporal peaks in food abundance (Alerstam et al. 2003). This migratory behavior is to a certain extent genetically engrained (Liedvogel et al. 2011; Merlin and Liedvogel 2019), such as, for example, the innate sense of direction and timing of migration in many passerines (Berthold and Helbig 1992). Yet, in recent years, evidence has rapidly mounted on how migratory behavior can also be shaped by experience (Mueller et al. 2013; Sergio et al. 2014; Campioni et al. 2020). This is most evident in species where migratory strategies are socially transmitted, such as, for instance, in

geese or cranes, and inexperienced young birds have to learn migratory routes and wintering sites on their first migration by following experienced individuals (Mueller et al. 2013; Oudman et al. 2018). However, even when migratory behavior has a strong genetic predisposition, individuals may benefit from experience. This is especially the case in long-lived species where migrations are repeated multiple times over an individual's lifetime, creating ample scope for learning (Guilford et al. 2011; Guilford and Burt de Perera 2017). Several recent studies on long-lived bird species indeed suggest an important role of experience as individuals were found to become less variable in their migratory behavior with age (Sergio et al. 2014; Campioni et al. 2020). However, till date, we still have little empirical evidence on how individuals ultimately use experience to trade off alternative options when taking en route decisions (Fayet 2020).

Address correspondence to J.M. Baert. E-mail: jan.baert@ugent.be.

*These authors shared last authorship.

In this study, we focus on the role of experience in the selection of stopover and wintering locations. This is an essential aspect for the viability of any migratory strategy as these locations have to yield sufficient rewards to offset the costs of migration (Lack 1968; Alerstam et al. 2003). Many species thereby seem to rely on experience with individuals often showing high fidelity to their stopover or wintering areas (e.g., Smith and Houghton 1984; Cantos and Tellería 1994; Harrison et al. 2010; Buchanan et al. 2012; Blackburn and Cresswell 2016). Such high stopover fidelity can be expected to be a particular favorable strategy if the distribution of resources is predictable across years. It may not only avoid costly detours in search of suitable stopover areas (Shaw and Couzin 2013) but also may strongly improve foraging efficiency within a stopover area by using prior knowledge about the spatiotemporal distribution of resources (MacArthur and Pianka 1966; McNamara and Houston 1985). But even when resources are less predictable, individuals may still benefit from revisiting known areas across years as familiarity with the area may aid them in finding foraging opportunities (Switzer 1993; Abrahms et al. 2018; Oudman et al. 2018; Morrison et al. 2021). However, experience may also play an important role in deciding when not to return and explore alternative, potentially better, options (Switzer 1993). Experience is, hence, expected to shape migratory strategies through a process of exploration and refinement (Guilford et al. 2011; Campioni et al. 2020; Fayet 2020). Individuals are likely most explorative early in life when chances of encountering better options are high, and progressively specialize on the best options when becoming older, and as such, become more experienced (Cresswell 2014; Fawcett and Frankenhuis 2015; Stamps and Frankenhuis 2016). But also later in life, individuals should also benefit from trading off costs and benefits of site fidelity and exploration as the profitability of foraging sites may change over time.

Here, we test this exploration-refinement hypothesis by assessing to what extent interannual variation in the selection of stopovers by adult lesser black-backed gulls, *Larus fuscus*, can be understood from

their experiences in the previous years. To this end, we analyze high-resolution GPS tracking data of 28 adult birds from three colonies in the southern bight of the North Sea that were tracked for at least two consecutive years. These long-lived birds present an interesting case study as their migratory strategies typically do not consist of a single seasonal movement between the breeding grounds and a single wintering area. Instead, movements outside of the breeding season consist out of a series of movements between long stopovers, from a couple of weeks up to several months (Figure 1, Baert et al. 2018; Brown et al. 2021). This may involve considerable detours with, for instance, many birds migrating north to the UK after the breeding season before moving southwards. Pronounced individual variation in migratory strategies thereby exists with some birds staying year-round in western Europe whereas others travel as far as West Africa (Klaassen et al. 2012; Baert et al. 2018). Despite these strong inter-individual differences in migratory strategies, it recently became clear that individual gulls do vary their migration behavior between years (Brown et al. 2021). This suggests that experience gained during previous years may play an important role in shaping their decision during current migration.

In this study, we focus on three main questions to explore how these birds may use experience during migration. First, we test if individuals rely on—and benefit from—experience during long stopovers (at least 7 days). As flight represents the bulk of the daily energy expenditure for these gulls even during stopovers (Shamoun-Baranes and van Loon 2006; Shamoun-Baranes et al. 2016, 2017), we expect that they should strongly benefit from using reliable food sources, either known from the previous year or newly discovered. Reliable food sources permit for high site-fidelity, which should permit for more efficient foraging by strongly reducing search efforts and thus the daily distance covered for foraging on these stopovers (MacArthur and Pianka 1966; McNamara and Houston 1985). In addition, we also expect that the reuse of foraging locations at stopovers across years may vary among migratory strategies. Long-distance migrants not only face an inherent uncertainty about the

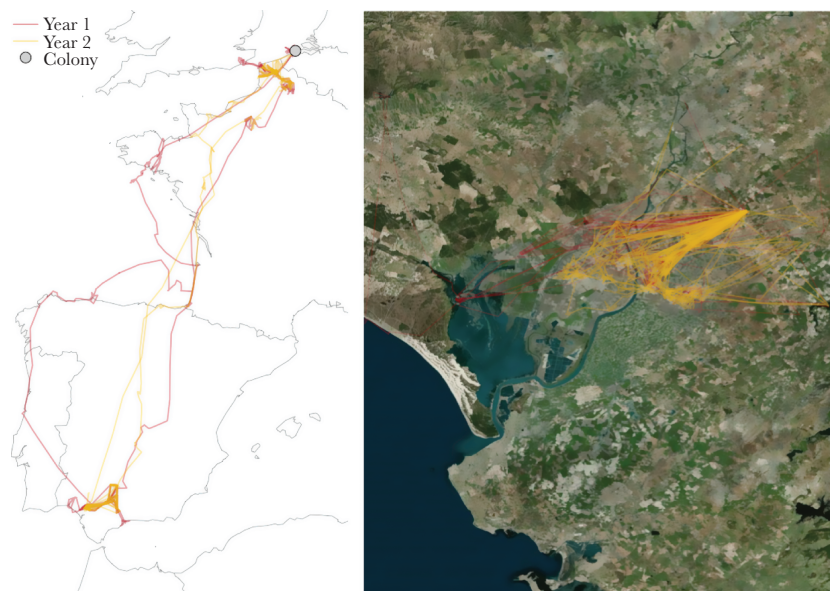


Figure 1

Illustration of the repeated migration by an adult Lesser Black-backed Gull (“L912685”) in two consecutive years (2014 and 2015). The right panel shows how the bird revisits stopovers in northern France and southern Spain. The left panel illustrates the similarity in foraging movements across the stopover in the Doñana area, southern Spain. Note the strong daily consistency in foraging commutes. Maps are created using OpenStreetMap data under the open database license.

conditions at their destination at the moment of departure, but also have to offset a higher energetic investment in migration. Hence, we expect food source reliability to play an increasingly important role for stopovers that lay further from the colony. To test these hypotheses, we quantify to what extent birds are reusing foraging sites from the previous year when revisiting a stopover, assess how this affects foraging site fidelity at the stopover and daily foraging effort and compare this to stopovers that were not visited in the previous year. Second, we assess if individuals may use experience from the previous year for stopover selection. To this end, we test if the revisiting probabilities of long stopovers (i.e., 7 days or more) depends on the site fidelity to foraging locations, and thus likely reliability of food sources used during stopovers in the previous year. Third, we test to what extent individual differences in interannual consistency in stopover use among gulls may thus be explained from individual differences in the reliability of food sources used on stopovers.

MATERIALS AND METHODS

GPS tracking

Between 2013 and 2018, 143 breeding adult (i.e., at least 4 years of age) Lesser Black-backed Gulls from three colonies along the Belgian-Dutch coast—Ostend ($n = 6$), Zeebrugge ($n = 79$), and Vlissingen ($n = 58$)—were fitted with GPS trackers. All birds were caught on the nest during incubation using walk-in traps or clap nets and equipped with solar-powered UvA-BiTS 5CDLe GPS trackers (Bouten et al. 2013). The deployment of GPS trackers was authorized by the ethical committee for animal experiments of the University of Antwerp (ID numbers CDE2013-73 for Zeebrugge and Ostend, and ECD2015-67 for Vlissingen) and conducted in accordance to Flemish, Belgian and Dutch legislation. Of these 143 birds, 80 birds returned the next year to the same colony. Note that because data could only be retrieved through a ground station in the colony, no data could be retrieved for birds that did not return to the colony. However, to be able to reliably derive migratory decisions, we only selected years with data gaps (because of empty batteries) less than 7 consecutive days for further analysis. This way, we retained 28 birds for which we had at least two consecutive complete years of tracking data: 16 birds from the Zeebrugge colony (8 males, 8 females), 9 from the Vlissingen colony (6 males, 3 females), and 3 from the Ostend colony (2 males, 1 females). Of these 28 birds, 3 were tracked for 5 consecutive years, 4 for 4 years, 7 for 3 years and 14 for 2 years (see also [Supplementary Table 1](#) for a complete overview of all tracked birds).

Data processing

Prior to any calculations, all tracking data was subsampled to a 30-min resolution to avoid any biases by the different resolutions at which the data was originally collected (resolution varied between 5 and 30 min). Next, we selected all data outside of the breeding season for each bird, which we defined as starting from the moment a bird last left the colony at the end of the breeding season until it returned to it in the next year. We then split this data into stopovers and migratory bouts using density-based spatial clustering of applications with noise (DBSCAN, for an illustration see [Supplementary Figure 1](#)), using the “dbscan” (Hahsler et al. 2019) package in R (R development core Team 2019). To achieve this, we set the neighborhood radius at 0.1 degrees (ca. 10 km) to be able to distinguish between repeated foraging movements within a stopover site and one-way migration bouts between stopover sites. As birds typically migrate at 30–40 km/h, this ensures that points do not cluster

during the unidirectional movement of migration but only when birds are performing repetitive movements during stopovers (see [Supplementary Figure 1a](#)). In addition, clusters were required to contain at least 48 data-points (i.e., birds had to spend at least 1 day on a stopover site). Next, we identified putative foraging locations for each day during stopovers ([Supplementary Figure 2](#)). Lesser Black-backed Gulls use a wide variety of food sources and foraging strategies, such as sit-and-wait strategies on dumpsites, foraging on foot in agricultural areas and actively tracking fishing vessels for spill overs (Sotillo et al. 2019; Spelt et al. 2019). While foraging strategies may thus vary in the extent by which they involve certain specific active behavior (for instance walking or soaring), they all typically result in a ground speed lower than the cruising speed they achieve when commuting between roosting and foraging sites, or when searching for foraging opportunities, resulting in a bimodal distribution of ground speeds with a cut-off around 5 m/s ([Supplementary Figure 3](#)). Similar to foraging, roosting also involves very low ground speeds. We identified these night roosts, on which birds were not assumed to forage, as the last location for each day where birds were inactive for at least 3 h uninterrupted. We considered birds to be inactive if the instantaneous ground speed measured by the accelerometer of the trackers did not exceed 0.5 m/s and birds stayed within a 1 km radius for at least 3 h.

For each day during a stopover, we then calculated the total distance covered, the fidelity to foraging sites and, for stopovers that have been revisited in the previous year, the reuse of foraging sites from the previous year. The total distance covered was calculated as the summed haversine distance between all GPS positions for a given day, and corrected for the coverage (i.e., the ratio between the number of GPS positions and the maximum possible number of positions, which is 48). The fidelity to foraging sites during a stopover was calculated as the proportion of GPS positions where the bird was assumed to be foraging, which lay within 500 m of a GPS position where the bird had been foraging within the previous 7 days. Similarly, for revisited stopovers, the reuse of foraging sites from the previous year was calculated as the proportion of GPS positions which were considered to be foraging, which lay within 500 m of a GPS position where birds had been foraging in the previous year. We use this 500 m cut-off to account for the potential account larger errors, up to over 100 m, when determining GPS positions at low temporal resolution (Bouten et al. 2013) as well as for the potentially large foraging locations used by these birds, such as fields or landfill sites, where birds may not be foraging on exactly the same spot in consecutive days or years. Stopovers were considered to be revisited when GPS positions of stopovers, as identified through the DBSCAN algorithm, overlapped in consecutive years. Throughout the whole analyses we only retained data for days with at least 12 h of data.

Data analysis

First, we assessed if individuals rely on experience to find food during a stopover, and whether this affected daily behavior in comparison to stopovers that were not visited in the previous year and whether this varies as stopover lie further from the colony. To this end, we used generalized mixed effects models to model temporal dynamics in the reuse of foraging locations across years for stopovers that were visited in the previous year. Next, to evaluate how this may affect behavior, we model temporal dynamics in foraging site fidelity and the daily distance covered for foraging for both stopovers that were and were not visited in the previous year. Temporal dynamics in all three models were estimated using

thin plate regression splines. Because we expect changes to primarily take place in the first days after arrival on a stopover, we modeled time as the decimal logarithm of the day since arrival on the stopover. All models also included the distance of a stopover from the colony as a fixed effect. For the models of daily foraging effort and site fidelity, we fitted a separate smoother for stopovers that were revisited in the previous year ($n = 105$), and stopovers which hadn't been visited in the previous year ($n = 28$) to be able to detect temporal differences among both. In addition, both models also included a Boolean indicating whether a stopover was visited or not visited in the previous year which was included as a fixed effect in these models to be able to test for differences in the average between both. All three models contained a first-order temporal autocorrelation structure and a random intercept for each individual and year to account for dependencies in our data. Observations were weighted based on the number of stopovers for which data was available to account for the decreasing sample size with stopover duration. Daily distances were modeled as a Gaussian distribution. Site fidelity during stopovers and reuse across years was modeled as a binomial distribution as nearly all values were either 1 or 0 since birds generally only used a single foraging location per day.

Next, we assessed if individuals may use the experience from the previous year for stopover selection. To this end, we tested for the 123 stops that were revisited and the 29 stops that were not revisited in the next year if revisiting probabilities varied in relation to the foraging site fidelity attained during a stopover in the previous year. We used a mixed effects logistic regression model including the average foraging site fidelity during a stopover in the focal year and the distance from the colony as fixed effects. We included the latter to be able to test if there are any differences in stopover revisiting probabilities among migratory strategies. In addition, individual and year were included as random intercepts.

Finally, we assessed to what extent fidelity to foraging locations, and thus likely the reliability of food sources, may ultimately drive individual differences in interannual variation in migratory behavior for the 28 birds included in this study. We therefore first calculated the interannual variation in migratory behavior for an individual. To this end, we determined for each day if the bird was visiting the same stopover in the previous years, and quantified interannual variation as the proportion of days outside of the breeding season where a bird was not revisiting the same

stopover from the previous year. We then used a mixed effects regression model to test if this interannual variation depended on the average foraging site fidelity during stopovers in the previous year. In addition, a random intercept for each individual and year was included in the model to account for dependence in the data. All models were fitted using the 'mgcv' package (Wood 2017).

RESULTS

Lesser Black-backed Gulls strongly relied on foraging locations from the previous year when revisiting stopovers in consecutive years. The probability of revisiting foraging locations used in the previous year thereby increased from on average 0.65 on the first day after arrival at a stopover up to 0.82 (Figure 2). In addition, this reuse of foraging locations across years was higher for stopovers that were located further from the colony (Table 1). As expected, gulls tend to rapidly develop high site fidelity at a stopover, which resulted in a concurrent decrease in the daily distance travelled for foraging (Figure 2). Site fidelity to foraging locations thereby increased most rapidly in the first 10 days after arrival on a stopover. In about 1 in 4 stopovers, birds already revisited a foraging site after the first day and foraging site fidelity subsequently steadily increased to an estimated mean of 0.70. However, while this increase in foraging site fidelity was similar between stopovers that were and were not visited in the previous year, average daily distances were significantly lower on stopovers that were visited in the previous year compared to stopovers that were not visited in the previous year with estimated means corresponding to 52 and 62 km/day, respectively. Note that although average daily distance appeared to increase again after 100 days on that were visited in the previous, such very long stopovers are rare. Estimates are thus based on progressively few stopovers as of the 133 stopovers included in the model only 38 are longer than 100 days and 15 longer than 150 days (Supplementary Figure 3).

As expected, Lesser Black-backed Gulls showed high fidelity to their migratory stopovers across years, with an estimated mean revisiting probability of 0.83. Revisiting probabilities of stopovers thereby strongly depended on foraging site fidelity attained in the previous year, with the stopover associated with the highest foraging site fidelity having a 53% higher probability to be revisited compared to stopovers with the lowest foraging site fidelity (Figure 3). In

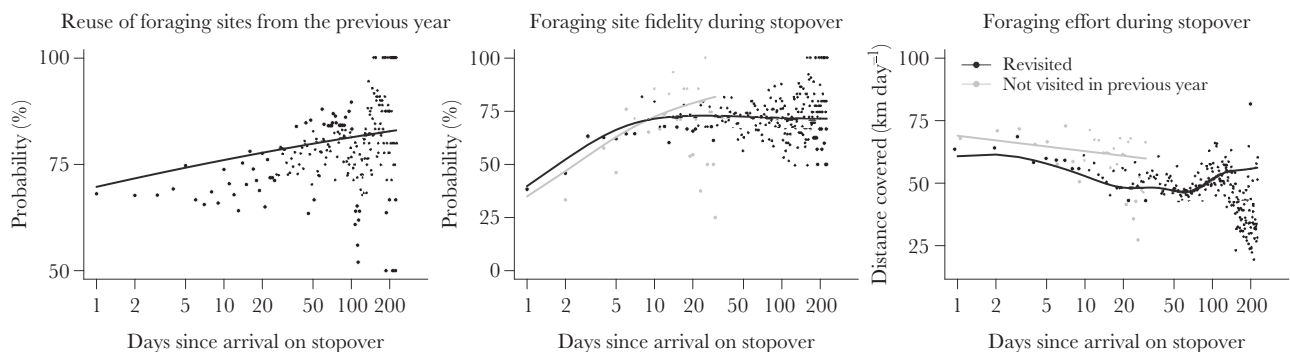


Figure 2

Foraging behavior during stopovers. The left panel shows the average reuse of foraging locations from the previous year when revisiting a stopover. The middle panel shows the average site fidelity to foraging locations during a stopover on both stopovers that were visited during the previous year (black) and stopovers that were not visited in the previous year (gray). The right panel shows the average daily foraging effort during stopovers for both stopovers that were visited during the previous year (black) and stopovers that were not visited in the previous year (gray). Points correspond to the mean values for each day. Additive mixed effects models are summarized in Table 1.

Table 1
Estimated fixed effects and test statistics of mixed effects models.

	Estimate \pm SE	df	χ^2 -statistic	P-value
Reuse of foraging sites across years during revisited stopover (-)				
Distance from colony	$4.30 \pm 0.56 \times 10^{-4}$	1	59.30	<0.01
$f(\log_{10} \text{ day})$		1.01	14.77	<0.01
Foraging site fidelity during stopover (-)				
Distance from colony	$1.85 \pm 4.20 \times 10^{-5}$	1	0.19	0.66
Revisited stopover	$-3.34 \pm 9.32 \times 10^{-2}$	1	1.42	0.23
$f_{\text{revisited}}(\log_{10} \text{ day})$		3.37	58.21	<0.01
$f_{\text{not visited}}(\log_{10} \text{ day})$		1.38	20.17	<0.01
Foraging effort during stopover (km/day)				
Distance from colony	$-3.98 \pm 4.96 \times 10^{-4}$	1	0.64	0.42
Revisited stopover	-9.53 ± 3.29	1	8.41	<0.01
$f_{\text{revisited}}(\log_{10} \text{ day})$		6.39	15.57	<0.01
$f_{\text{not visited}}(\log_{10} \text{ day})$		1.01	2.78	0.09
Stopover revisiting probability				
Foragingsite fidelity	3.15 ± 1.21	1	6.726	<0.01
Distance from colony	$3.68 \pm 1.82 \times 10^{-4}$	1	4.096	0.04
Interannual consistency in stopover use (-)				
Foraging site fidelity previous year	-0.88 ± 0.26	1	11.72	<0.01

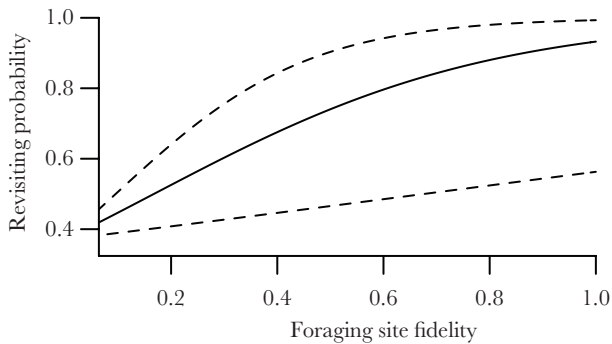


Figure 3
 Estimated effect of the average foraging site fidelity during a stopover on the probability a stopover will be revisited in the next year. The solid corresponds to the mean model prediction, the dotted lines correspond to the 90% prediction interval. The generalized additive mixed effects model is summarized in Table 1.

addition, revisiting probabilities also varied to a lesser extent based on the distance to the colony with the further stopovers having up to 30% higher revisiting probabilities compared to stopovers close to the colony (Table 1).

Consistent with this pronounced effect of foraging site fidelity on the revisiting probability of individual stopovers, the average foraging site fidelity of an individual across its stopovers also related to individual differences in interannual variation in migratory behavior (Figure 4, Table 1). Birds that showed an on average higher foraging site fidelity on stopovers showed significantly less interannual variation in their stopover use. Birds showing the highest average foraging site fidelity thereby spend up to 85% of their time spent on the same stopover they visited at the same date in the previous year, whereas this was on average 53% for birds showing the lowest average foraging site fidelity on stopovers.

DISCUSSION

Our results demonstrate how Lesser Black-backed Gulls use, and benefit from experience, both during stopovers and across years. While it has been known that Lesser Black-backed Gulls

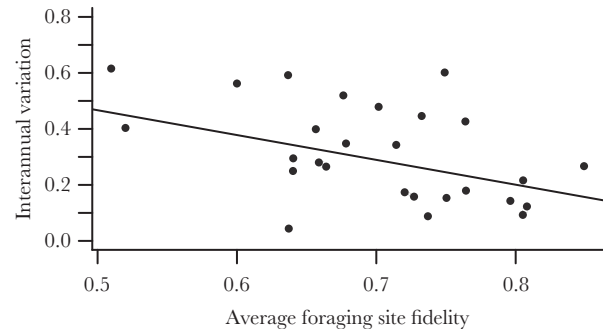


Figure 4
 Estimated effect of the average foraging site fidelity on stopovers on the interannual variation in stopover used. Points represent the average value for each individual. The linear mixed effects model is summarized in Table 1.

are generally highly consistent in their migratory behavior across years, with major changes in migration routes being extremely rare (Brown et al. 2021), very little has so far been known on the underlying drivers of interannual variation in the migratory behavior of individual gulls. Our analyses support the idea that these interannual changes may be understood from a process of exploration and refinement, whereby birds are more likely to retain favorable stopovers from the previous year and abandon less favorable stopovers to explore alternatives (Guilford et al. 2011; Fayet 2020). Food source reliability thereby appeared to play a major role in these decisions. As generally predicted from an optimal foraging perspective (MacArthur and Pianka 1966; McNamara and Houston 1985, 1987; Switzer 1993), birds strongly benefited from a high fidelity to foraging locations during stopovers as this enabled them to simply commute between roosts and foraging locations (Figure 1), thereby reducing the daily distance covered for foraging by largely omitting the need for searching (Figure 2). Birds also tend to strongly rely on experience from the previous year as gulls strongly reused foraging locations from the previous year when revisiting a stopover. Upon arrival at a stopover site, over 65% of the foraging trips were directed toward foraging locations used in the

previous year. This further increased to an average of 82% after a few days (Figure 2). In addition, revisited stopovers required on average a lower daily foraging effort compared to stopovers that were not visited in the previous year (Figure 2).

Furthermore, our results show that interannual variation in migratory behavior of individual gulls depends on the foraging site fidelity attained on stopovers in the previous year. While gulls were generally very consistent in their migratory behavior across years with an average stopover revisiting probability of 83% (Figure 3), revisiting probabilities varied by over 50% in relation to the average foraging site fidelity during stopovers in the previous year (Figure 3). Accordingly, birds using stopovers associated with high foraging site fidelity, and thus likely highly reliable resources, showed very little interannual variation in stopover use (Figure 4). They thereby spend up to over 85% of their days on the same stopover they visited at the same date in the previous year, whereas this could be less than 40% for birds showing the lowest foraging site fidelity.

While birds thus clearly benefitted from using reliable resources as it enabled them both to forage more efficiently during stopovers and to reuse stopovers across years, little remains known on what ultimately drives resource selection in these birds. Lesser Black-backed Gulls are known to use a wide range of natural and anthropogenic food sources, which have inherent differences in their spatiotemporal predictability. For example, many Lesser Black-backed Gulls wintering in West Africa fish for themselves (Camphuysen and van der Meer 2005) in coastal upwelling zones where the exact distribution of their food may vary between years. Most anthropogenic food sources are instead highly predictable. Farming activities, for example, typically create spatially predictable, temporal peaks in food availability. Many Lesser Black-backed Gulls, for instance, visit the Doñana area in southern Spain during the rice harvest at the beginning of winter as the exposure of crustaceans due to farming activities provides an easy meal (Martín-Vélez et al. 2020). Urban and industrial food sources, such as dump containers and landfills, likely present the most reliable food sources as food is available at specific locations often year-round. While high site fidelity offers the clear advantage of a lower energetic investment in searching, we have no information on the energetic returns. In addition, individual specialization is also often associated with increased foraging efficiency as experience may reduce searching and handling times (Araújo et al. 2011). Hence, higher interannual variation may be the result of either suboptimal stopover selection or of birds preferring resources that are generally less predictable in time and space.

Our results suggest that migratory behavior across years is to a large extent influenced by learning about specific foraging opportunities, which is unlikely to be innate. As birds clearly benefitted from experience through a reduced foraging effort, this raises important questions on the relative importance of learning and innate behavioral responses on the ontogeny and adaptive value of migratory strategies. Despite most species having some learning capacity (Boogert et al. 2018; Poirier et al. 2020), its impact on behavioral variation has long been overlooked (Snell-Rood 2013; Snell-Rood and Steck 2019). This includes individual variation in migratory behavior. Ever since David Lack's first treatise on the subject (Lack 1968), this variation has predominantly been considered from an evolutionary perspective, assuming that strategies coexist because of fitness equivalence (Lack 1968; Lundberg 1987), or represent distinctive optimal strategies in relation to age, size, or sex (Ketterson and Nolan 1983). A recent study on individual variation in the migratory behavior of Lesser Black-backed Gulls did indeed find some support for fitness equivalence among migratory strategies as they

found that long-distance and short distance migrants, covered on average the same total distance per year (Shamoun-Baranes et al. 2017). Individuals performing long-distance migrations therefore appear to benefit from a lower foraging effort at their destination, compensating for their higher energetic investment in migration to cover these distances. However, the total distance covered varied strongly among individuals with similar migratory strategies (Shamoun-Baranes et al. 2017) and a successive study also revealed pronounced individual differences in interannual consistency in migratory behavior (Brown et al. 2021). Our results suggest that both individual and interannual variation could be understood from individual experience.

However, our data only provides a snapshot in the lives of these birds. These gulls may well live up to 20 years of age (Camphuysen 2013), and all birds reproductively active adults at the moment of tracker deployment. While our analyses clearly show how birds use experience when revisiting stopovers across years, we do lack some important information to understand how birds select stopovers that were not visited in the previous year. These stopovers could be completely new, but could also be known from earlier years. For instance, we find that although birds develop similar levels of foraging site fidelity both at stopovers that were and were not visited in the previous year, the latter were associated with greater daily foraging distances (Table 1, Figure 2). This could be because these are more unfavorable stopovers that birds have skipped for some years and birds may thus benefit from familiarity with the site. However, even if birds are indeed exploring new sites, such increase site fidelity can be expected. Exploration is energy demanding, so birds may be simply forced to rapidly specialize after arrival to replenish energy reserves after migration, even when this does not represent the best option (Shimada et al. 2020). Alternatively, birds could use social information, and rapidly learn about the best foraging options within an area from their already present conspecifics.

Understanding how stopover selection is affected by experiences during the first migration is therefore an important next step. Individuals are generally most sensitive to novel information early in life (Fawcett and Frankenhuis 2015; Stamps and Frankenhuis 2016). Individuals may thus predominantly refine their migratory decisions based on their experiences during their first migration, which is known as the serial residency hypothesis (Cresswell 2014). Moreover, often these first migrations are susceptible to stochastic events, such as wind conditions, which ultimately determine, if or which suitable stopovers they encounter during this first migration. As Lesser Black-backed Gulls often migrate in loose flocks, social learning may also play an important role during this first migration. In a recent study, Borrmann et al. (2021) showed high similarity in the migratory behaviour and stopover selection between juvenile and adult birds, suggesting an important role of social learning. In addition, Pütz et al. (2008) showed high consistency in migratory behavior across the lifetime of a single Lesser Black-backed Gull tracked from the moment of fledging until adulthood. Combined, these studies hint toward major effects of early life events. However, more detailed studies with pedigree information will be needed to fully disentangle the relative contribution of genetics and learning to individual variation in migratory behavior in these gulls.

In conclusion, adult Lesser Black-backed Gulls within our study showed high interannual foraging site fidelity during migration, suggesting strong dependence on experience. We also found pronounced individual variation in the extent by which they did so and this strongly affected the foraging effort during migratory stopovers,

the chances that stopovers were revisited in consecutive years and accordingly individual differences in interannual variation in migratory behavior. Hence, our results not only add to the mounting evidence of the importance of experience for long-lived species, it also raises important questions on the ultimate role of experience on the development of migratory behavior in these gulls, as well as on the relative importance of genetic factor for the adaptive value of migratory strategies. This stresses the need for studies that track individuals from a young age to deepen our understanding of how phylogenetic and ontogenetic adaption shape behavioral variation within populations.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This work was supported by the grants of the Research Foundation Flanders to J.M.B. (12R7619N) and to L.L. and W.M. (G0E1614N), and makes use of data and infrastructure provided by the Flemish Marine Institute (VLIZ) and Research Institute for Nature and Forest (INBO), which was also funded by Research Foundation Flanders (FWO) as part of the Belgian contribution to LifeWatch. FV and LL are currently supported by Methusalem Project 01M00221 (Ghent University)

We thank Wouter Courtens, Roland-Jan Buijs, Marwa Kavelaars, Hans Matheve and Reyes Salas for their support in the field, the Port of Zeebrugge and Zeeland Seaports for their permission to access the port, and COVRA, EPZ, Pacorini, and Van Citters Beheer BV for access to their sites.

ETHICS STATEMENT

The deployment of GPS trackers was authorised by the ethical committee for animal experiments of the University of Antwerp (ID numbers CDE2013–73 for Zeebrugge and Ostend, and ECD2015–67 for Vlissingen) and conducted in accordance to Flemish, Belgian and Dutch legislation.

AUTHOR CONTRIBUTIONS

J.M.B. and W.M. designed the study. J.M.B. carried out all analyses. All authors contributed to the writing of the manuscript.

Data availability: Analyses reported in this article can be reproduced using the data provided by Baert et al. (2021). All GPS data used in this study are publicly available in Movebank and Zenodo (<https://doi.org/10.5281/zenodo.3540799>).

Handling Editor: Leigh W. Simmons

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