Original Article

First explorations: ontogeny of central place foraging directions in two tropical seabirds

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A widespread hypothesis for the ontogeny of behavior and decision-making is the early-exploration-later-canalization hypothesis. It postulates that juveniles are more exploratory and adults more consistent in their behavior. In addition, it is often assumed that naïve juveniles could overcome the costs of individual experience building by copying more the decisions of others than adults (early-conformism-later-self-defining hypothesis). Here, we compare the central place foraging movements of adults and postfledging juveniles in their first flights around the colony before dispersal and migration in two sympatric species of tropical seabirds: red-footed boobies and great frigatebirds. Using GPS records of individual movements, we analyzed the foraging directions of seabirds from the colony across successive trips. Juveniles of both species showed significant within-individual consistency in foraging direction but at lower levels than adults. Juveniles leaving the colony within the same time window showed significant but low between-individual resemblance in foraging direction at levels similar to adults. In both species, homing efficiency was lower in juveniles than in adults. Juvenile foraging directions were initially influenced by wind conditions, particularly in low wing loading frigatebirds. Wind conditions progressively lost influence on juvenile foraging directions during their first weeks of flights. In contrast, within-individual consistency, between-individual resemblance, and homing efficiency did not show signs of progression in juveniles. Our results support the early-exploration-later-canalization hypothesis but not the early-conformism-later-self-defining hypothesis. Relaxed constraints on self-feeding efficiency could favor high variability in postfledging tropical seabirds. Our simple approach could be applied to further test these hypotheses by comparing strategies across a wide range of central place foragers.

Lay Summary: Juvenile tropical seabirds were more exploratory but not more conformist than their parents in their successive excursions out of the colony. Yet juveniles homed less efficiently and were more affected by wind conditions than adults. Species differed in how juveniles used wind in early flights, consistent with their soaring flight style. The exploratory behavior in juveniles might be favored in these species through persistent parental feeding of fledged juveniles.

Key words: **coloniality, homing efficiency, ontogeny of foraging decisions, postfledging juveniles, tropical seabirds, wind use.**

INTRODUCTION

When becoming independent from parental care, juveniles face an environment they have low experience of, but from which they must obtain resources needed for survival (Cox et al. 2014; Wunderle 1991). Some of the foraging skills used by adults may require a long developmental phase, but some other behaviors expressed by adults may be in place as soon as the juvenile starts to explore its environment (Wunderle 1991; McFarland 1999: p. 3). In many species, juveniles can remain bounded to their birthplace for some time before they are able to move independently to disperse or migrate ("postfledging phase" in birds; Cox et al. 2014).

At this period, adults and juveniles simultaneously experience the same local environment, allowing for a direct comparison of their respective strategies at a fine scale. Yet, this phase is challenging to document in wild animals (Baker 1993; Cox et al. 2014), despite being critical for their life history because high mortality occurs at this stage (Gaillard et al. 1998; Daunt et al. 2007).

When leaving from a central place to forage, both juveniles and adults make decisions on where to go. These decisions may or may not be influenced by their previous personal experience, leading to high or low individual consistency. Decisions may also be influenced by environmental or social cues directly perceived when making the decision. As a result of these processes, an individual's decision may or may not resemble that of other neighboring individuals at the same time, leading to either high or low

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between-individual differences. In addition, when making these decisions, individuals must deal with potentially strong environmental constraints that could restrict their choices (Oppel, Dobrev, et al. 2015; Sherley et al. 2017; Yamamoto et al. 2017) and they must efficiently orientate to home back to their central place (Capaldi et al. 2000; Mandal et al. 2017; Mandal et al. 2018). How naïve juveniles moving alone or in groups weigh these alternative decisions and manage these constraints and how these skills develop and compare with adult behavior is still poorly known, especially for wild, wide-ranging animals, such as seabirds that cannot be observed at sea (Capaldi et al. 2000; Hazen et al. 2012; Mendez et al. 2017; Votier et al. 2017).

A strategy based on individual consistency to a spatial area could allow the individual to gain advantages from its personal knowledge of this local environment (Dukas 1998; Patrick and Weimerskirch 2014; Mandal et al. 2017). Should the local conditions change however, high consistency could reveal costly compared with a more exploratory strategy (Dukas 1998; Patrick and Weimerskirch 2014; Sherratt and Morand-Ferron 2018). A widespread hypothesis is that, during their lifetime, individuals follow an early-exploration-later-canalization strategy (e.g., Guilford et al. 2011; Votier et al. 2017; Sherratt and Morand-Ferron 2018): naïve individuals start by exploring various sectors to probe their environment and only later start to specialize into a consistent, narrower area (hypothesis 1a: initially low but increasing within-individual consistency). Alternatively, young individuals might initially display high foraging site consistency, before being able to exploit a wider range of conditions during adulthood (hypothesis 1b or "early-focus-later-generalization": initially strong within-individual consistency but decreasing throughout lifetime: (Oppel, Dobrev, et al. 2015; Sherley et al. 2017). Finally, foraging-site consistency strategies may not be influenced by age and remain constant throughout the lifespan of an individual (hypothesis 1c: constant within-individual consistency).

When individuals make a decision on where to forage, this may or may not resemble the decisions of other individuals at the same time (Bolnick et al. 2003; Guilford et al. 2011; Patrick and Weimerskirch 2014; Votier et al. 2017) whether or not individuals show consistency in decisions. This could result, for a given period of observation, in apparent "population-level" preferences for a finite number of decisions among all potential choices. Sharing the same decisions and foraging areas with neighbors could better allow individuals to bypass costs of individual trial-and-error (Dukas 1998) and may enable learning from potentially more knowledgeable individuals (Dukas 1998; Kendal et al. 2005). This may be important for juveniles lacking personal information compared with adults (hypothesis 2a or early-conformism-later-self-defining hypothesis: initially high resemblance between individuals but decreasing throughout life; Mendez et al. 2017). On the other hand, sharing the same foraging decisions with neighbors could largely increase foraging competition between individuals. Individuals that would avoid following "population-level preferences" ("anticonformist" strategy) may decrease the level of competition they experience and be favored by evolution (Kendal et al. 2005; Patrick and Weimerskirch 2014). This could apply equally to juveniles and adults, and we may, therefore, observe low resemblance between individuals constant throughout life stages (hypothesis 2b).

After foraging, central place animals need to find their way back to the colony (Degen et al. 2016; Mandal et al. 2017). Some navigational processes may not be innately mastered; for instance, the use of landmarks is likely to require a learning phase as these landmarks should be colony dependent (Degen et al. 2016). However, other navigation mechanisms could allow innate homing (Cheng et al. 2014); for instance, the use of path integration (constantly updating the distance and direction from the colony while moving). Although homing capacities and their ontogeny have been relatively well studied in several wild colonial hymenopterans (Capaldi et al. 2000; Cheng et al. 2014; Woodgate et al. 2016; Mandal et al. 2017), the homing capacities of postfledging birds before dispersal or migration are much less known.

Finally, all these predictions might be confounded by the effects of strong environmental constraints, such as wind. Wind could restrict movement choices to particular areas or directions and/or wind could affect flight and, therefore, homing performances (Spear and Ainley 1997; Yamamoto et al. 2017). This may also confound the comparison between juveniles and adults if juveniles require a learning phase to overcome wind constraints (Riotte-Lambert and Weimerskirch 2013; Harel et al. 2016; De Grissac et al. 2017).

Here, we investigated the change over time in the movement decisions and homing behavior of juvenile postfledging tropical seabirds in their early flights at sea around the colony. We attached miniature GPS to adults and juveniles of two sympatric species to compare their movement behavior. We tested for each species the five hypotheses above (summarized in Table 1) relating to within-individual consistency and between-individual resemblance in foraging direction, and we compared homing performances of adults and juveniles. To further test whether observed behaviors reflected individual decisions rather than a lack of choice from external environmental constraints, we explicitly accounted for wind conditions in our analyses of movement. We studied great frigatebirds (*Fregata minor*) and red-footed boobies (*Sula sula*) nesting in Europa Island, Mozambique Channel. Both species feed on similar prey in oceanic tropical waters characterized by low productivity (Mendez et al. 2016), a relatively ephemeral and dynamic resource distribution (Weimerskirch et al. 2005; Weimerskirch 2007), and, presumably, a paucity of prominent landmarks away from the colony (Guilford et al. 2011). We expected contrasting results between these two species as they notably differ in their social behavior (red-footed boobies often leave the colony in small groups (Nelson 2005; Mendez et al. 2017)) and also in their flight mechanics. Horizontal winds may act as an energetic help for flight in red-footed boobies relying on dynamic soaring at low altitude (Ballance 1995; Weimerskirch et al. 2005). Horizontal winds may rather be a locomotion constraint for frigatebirds relying on ascending air to gain high altitudes before they can glide at virtually no energetic costs (Weimerskirch et al. 2016). We expected species to differ on their wind preferences and on their propensity to display between-individual resemblance, but we had no prior expectations on potential age effects on such interspecies differences.

MATERIALS AND METHODS
GPS-logger deployment

In January and February 2014 and 2015, 12 adult frigatebirds and 18 adult red-footed boobies were fitted with GPS tags on Europa Island, Mozambique Channel (22.37°S, 40.36°E). In frigatebirds, solar-powered GPS (PS-RF, e-obs GmbH, Munich, Germany) weighed 30 g and recorded points every 2 or 5 min for a total of 335 complete tracks. In red-footed boobies, battery-powered GPS (I-GotU, Mobile Action Technology Inc., Taiwan) weighed 20 g and recorded points every 2 min for a total of 111 complete tracks.

Table 1

Summary of hypotheses, predictions, and results for the comparison of juveniles and adults. Supported hypothesis are highlighted in bold and gray shading

Hypothesis	Predictions	Results
	Within-individual consistency	
Early-exploration-later-canalization	Juveniles < adults	Juveniles < adults
Early-focus-later-generalization	Juveniles > adults	
No age-related effects	Juveniles = adults	
	Between-individual resemblance	
Early-conformism-later-self-defining	Juveniles > adults	Juveniles = adults, low value but above
Anticonformist strategy	Juveniles = adults, value at or under random expectations	random expectations
	Homing efficiency	
Innate mechanisms (e.g., path integration)	Juveniles = adults	Juveniles < adults (flight capacities as
Learnt mechanisms (e.g., use of landmarks)	Juveniles < adults	confounding factor)
	Wind influence	
Primary constraint restricting choice of foraging direction	High individual resemblance and wind-dependent individual consistency	Low individual resemblance, individual consistency weakly affected by wind
Learning phase to overcome wind constraints	Higher wind influence on juveniles than adults	(SI), and wind influence on juveniles but not on adults

Overall, the mass of attached devices weighed less than 2% of adult body mass (Weimerskirch et al. 2016; Mendez et al. 2017). Birds were captured with a noosed pole; twice for red-footed boobies (tag deployment and recovery) and only once for frigatebirds (remote data download). Individuals were randomly selected among easily accessible nests.

Young fledglings starting their first flights at sea were randomly selected and fitted with the same devices as their parents. Devices also represented less than 2% of body mass and recorded locations every 1 min. In total, 34 juvenile red-footed boobies were equipped in 2014 and 10 juvenile frigatebirds were equipped in 2015. Differences in juveniles between species might partly reflect year differences, but investigated adult behaviors of each species did not differ between years, and the average across years was used (see also Supplementary Material).

These procedures were approved by the Préfet des Terres Australes et Antarctiques Françaises in agreement with ethical guidelines and legislative regulations and were approved by the ethical committee of the funders. Birds were handled for less than 10 min and no nest desertion resulted from their captures. Previous work on seabirds has shown that using loggers with adapted mass, shape, and attachment procedure has very low impacts on individual behavior and demographic traits. Previous analyses of our data on juvenile behavior suggested that they did not behave differently from nonmanipulated juveniles (Mendez et al. 2017).

Defining and characterizing foraging trips at sea

We considered only the foraging trips at sea (>3 km) and not the short movements over land made by juveniles. For each foraging trip, we identified the most distant point from the colony ("maximum range") and extracted its great circle direction from the colony (relative to North, R package geosphere; Hijmans et al. 2015). We used this direction at maximum range to analyze the overall trip direction decision. This simplification of track complexity integrates all movement decisions from the departure to this point of maximum range. We consider this simplification representative of the whole trip because seabird trips, including those in the present study (see Results), are most generally of a "commuting" rather than "looping" type (Weimerskirch 2007): a given foraging trip rarely explores a wide range of directions around the colony but rather shows highly directional movements to and from a distal foraging area. Using the direction at maximum range instead of the direction at a fixed distance from the colony enables to keep all trips for analyses, regardless of their range. In Supplementary Material S3, we show that conclusions would be unchanged if we instead defined direction at a common and fixed distance from the colony (e.g., first 10 km). We discarded incomplete tracks where the direction could not reliably be estimated (last recorded point more than half the maximum range distance from the colony) and tracks during a cyclone with abnormal ranges (Mendez et al. 2017).

Within-individual consistency and between-individual resemblance

From the directions at maximum range, we could calculate angles between specific pairs of trips to evaluate whether paired trips shared a similar direction. To evaluate within-individual consistency, we considered pairs of successive trips of the same individual (number of pairs in juv. frigatebirds: 896; in juv. boobies: 239; in ad. frigatebirds: 318; and in ad. boobies: 88). For instance, considering trips 1, 2, 3, and 4 of an individual, we extracted the angles between trips 1 and 2, trips 2 and 3, trips 3 and 4, and so forth. To evaluate between-individual resemblance in foraging decisions, we considered pairs of "simultaneous" trips of different individuals leaving the colony within the same time window (number of pairs in juv. frigatebirds: 2183; in juv. boobies: 1576; in ad. frigatebirds: 280; and in ad. boobies: 88). We defined "simultaneous" as trips departing within 3 h of each other. A shorter temporal window threshold for "simultaneity" in departure increased the chance of individuals sharing a similar direction but reduced the sample size. We used a 3 h value as a compromise. In Supplementary Material S3, we show results when using other "simultaneity thresholds."

Wind

We downloaded 6-hourly wind data available at the resolution of 0.25° from the NOAA web repository (https://www.ncdc.noaa.gov/data-access/marineocean-data/blended-global/blended-sea-winds). This provides estimates of horizontal wind strength and direction at 10 m above the sea surface, from blending multiple-satellite imagery. We averaged for each 6-h period the direction and strength of wind within a 1°-square centered on the colony

and associated these values to all foraging trips departing during this period. Our measures are, thus, of coarse-scale wind conditions around the colony at foraging departure.

For each trip, we calculated the angle between the average wind direction and the direction from the colony to the point of maximum range. An angle of 180° indicated front winds and 0° indicated tail winds. For homing analyses only, wind conditions at the end date of foraging trips were used (rather than start date), and relative wind directions were calculated using the direction from the point of maximum range to the colony (i.e., homing direction).

Homing measures

To evaluate homing efficiency, we used two classical measures: trip straightness and average speed. We considered that the straighter and quicker the homing journey, the more efficient the homing. To enable meaningful comparisons between adults and juveniles, with different and variable foraging ranges (Mendez et al. 2017; Figure 1), we considered measures calculated on the last 30 km of trips (i.e., from the last point >30 km from the colony to the colony). This discarded trips with maximum range <30 km (i.e.,

many of the earliest trips of juveniles). Repeating this analysis on the last 10, 20, or 50 km did not qualitatively change the results.

Average speed is simply the average of speeds calculated between each consecutive GPS locations during the last 30 km. Straightness is the ratio of the beeline distance between the start and endpoint and the sum of distances between each consecutive GPS locations in between (i.e., "actual distance traveled"). It ranges between 1 (actual distance traveled = beeline distance) and 0 (distance traveled much larger than beeline distance). This measure is highly sensitive to the frequency of GPS recordings. We standardized recording frequency by downsampling all tracks to a 5-min frequency. Downsampled tracks with less than 10 intermediate locations for the last 30 km were discarded from homing analyses (number of analyzed homing phases in juv. frigatebirds: 178; in juv. boobies: 25; in ad. frigatebirds: 110; and in ad. boobies: 54).

Statistical models

Data and codes for statistical analyses are available as Supplementary Material. Our analyses for decisions on trip directions were based on angles between pairs of directions (e.g., angle
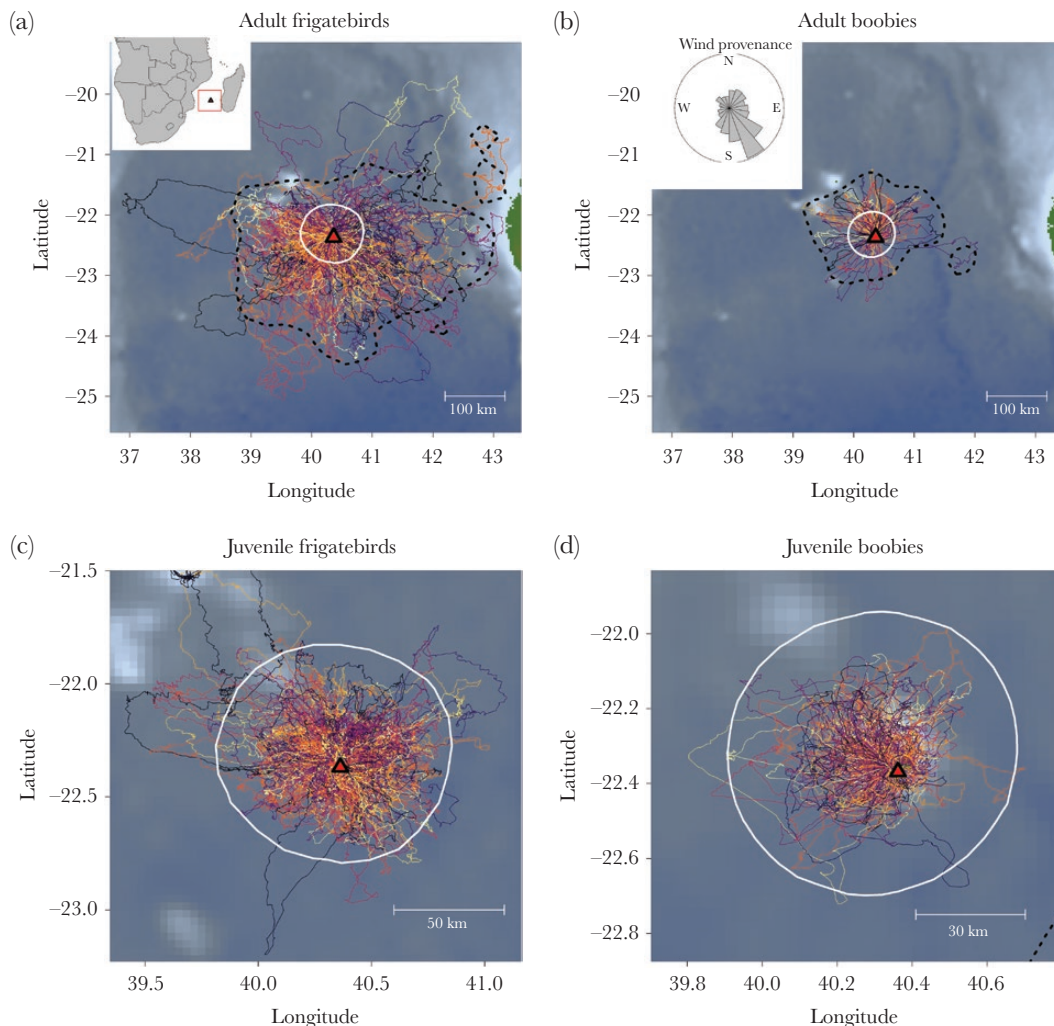

Figure 1

Adult (a, b) and juvenile (c, d) foraging trips (colored lines) and at-sea distribution (90% kernel contours) of adults (dashed black line) and juveniles (solid white line) in frigatebirds (a, c) and boobies (b, d) from Europa Island (red triangle) within the Mozambique Channel [top left inset in (a)]. Inset in (b) indicates the wind provenance direction during the study period (January–May of 2014-2015). Blue shades on map indicate bathymetry (R package marmap [Pante and Simon-Bouhet 2013]).

between two consecutive trips for within-individual consistency; see Homing measures) to avoid using circular statistics. Working on angles between trip directions rather than on measures of metric distance between foraging sites (e.g., Mendez et al. 2017; Votier et al. 2017) enables us to compare these angles to a realistic null mathematical distribution, chosen independently from the data. Assuming that all directions around the colony were a priori possible (see Results), we expected a uniform distribution between 0° and 180° for these angles under the null hypothesis. A 0°-skewed distribution of angles would indicate pairs of trips sharing a similar direction and, on the opposite, a deficit of values close to 0° compared with the null distribution would indicate avoidance between paired trips. The use of angles, thus, allows us to analyze separately individual consistency from individual resemblance in contrast to most previous studies on the subject where individual consistency is evaluated relative to between-individual variance (e.g., Bolnick et al. 2003; Patrick and Weimerskirch 2014; Votier et al. 2017).

To test whether angle distributions deviated from a uniform distribution around 0°, we used χ^2 tests. To assess whether biases differed between age classes (adults vs. juveniles), or changed through time in juveniles, we used binomial generalized linear mixed models (R package lme4; Bates et al. 2015: p. 4) taking bird identity as a random effect. For both binomial GLMM and χ^2 tests, the response variable was a categorical variable as either above or below a threshold angle of 30°. Using a threshold of 10° or 50° did not qualitatively change our conclusions (Supplementary Material S3).

Specifically, for each species and each measure (within-individual-consistency, between-individual resemblance, and use of tail and front wind), we developed one model comparing adult values with juvenile values and one model investigating changes through time in juveniles only. For the latter, we used the Julian date with the first tracking day as the origin.

Average speed and straightness were likewise analyzed in two steps, first comparing adults and juveniles within each species; then, investigating time progression in juveniles. We used Gaussian linear mixed models (R package nlme; Pinheiro et al. 2016) for both variables and, although the upper bound of straightness distributions slightly affected the variance of residuals, we do not believe that it can significantly affect our conclusions.

For each of these models, we incorporated wind direction and wind strength as covariates, as well as the maximum range from the colony. Results on the effects of these covariates are only reported in Supplementary Material S3 as beyond the primary scope of this paper. As it remains a possibility that tracked juveniles were of slightly different age and, although this would be partly controlled for by the individual random intercept, we ran models with the Julian date replaced by the trip number (in individual-based chronological order); this did not affect the conclusions.

RESULTS

Adults and juveniles of both species ranged in every direction from the colony, but juveniles made much shorter trips than adults (Figure 1; further details on juvenile trips are presented in Supplementary Material S1 and S2). Juveniles progressively increased their maximum range from the colony in both species (frigatebirds: 3.31 km + 0.25 ± 0.02 km/day, $t = 13.186$, degrees of freedom [df] = 918, $P < 0.001$; boobies: 10.8 km + 0.34 ± 0.06 km/day, $t = 6.153$, df = 287, $P < 0.001$). Results in Mendez et al. (2017) and Corbeau et al. (2020) provide more details on these juvenile maximum ranges. Overall, the direction at maximum range

was representative of the foraging trip direction: the trip direction at maximum range correlated with the direction of the first 10 km of trips (circular Pearson's product coefficient of correlation; in adult frigatebirds: 0.80, adult boobies: 0.85, juvenile frigatebirds: 0.85, juvenile boobies: 0.85; P-values <0.001 for each age-species class). Moreover, the majority of locations within a trip had a direction from the colony similar to that at maximum range (proportion of locations within 30° of direction at maximum range in adult frigatebirds: 80.2 ± 18.8%, juvenile frigatebirds: 70.0 ± 22.8%, adult boobies: 88.8 ± 16.6%, and juvenile boobies: 80.3 ± 20.8%).

The wind was predominantly blowing toward north-west during the study period (Figure 1b, inset). Birds experienced winds blowing at an average of 21.3 ± 9.7 km/h (range 1.1–49.5 km/h), with great variability all along each season (Supplementary Material S3). Overall, wind direction had weak effects on adult departure direction in both species (Figures 2a and 3a), with only a slight avoidance of tail wind directions in adult frigatebirds (10.9% of trip directions within 30° of wind direction, $\chi^2 = 4.198$, df = 1, $P = 0.04$; tests for tail wind direction in boobies or front wind directions in both species: $P > 0.21$). These results held true when considering apart strong or low winds (i.e., above or below median wind speeds; Supplementary Material S3). In both species, adults often returned in a similar direction (<30°) as the direction taken during their previous trip (within-individual consistency: frigatebirds: 49.7% of cases; boobies: 45.5%; no interspecific difference: z = −0.702, $P = 0.48$; Figures 2b and 3b). Adults "simultaneously" leaving the colony (<3 h) had a probability of taking similar directions (<30°) higher than expected by chance in frigatebirds but not red-footed boobies (between-individual resemblance: frigatebirds: 28.3%, $\chi^2 = 6.090$, df = 1, $P = 0.01$; boobies: 23.1%, $\chi^2 = 0.329$, df = 1, $P = 0.57$; no interspecific difference: $\chi^2 = 0.323$, df = 1, $P = 0.57$; Figures 2c and 3c). When using a more restrictive "simultaneity threshold" (1 h), individual adults leaving simultaneously were more likely to share a similar direction in frigatebirds (resemblance: 36.4% chance in frigatebirds, 20% in boobies; Supplementary Material S3). Conversely, when adopting a relaxed simultaneity threshold (6 h), the probability that two simultaneously leaving adult individuals would share a similar direction decreased in both species (Supplementary Material S3).

During earlier flights, juvenile frigatebirds (Figure 2a) frequently departed with tail wind directions (32.8% over the whole tracking period) in contrast with adult behavior (1.50 ± 0.33, z = 4.580, $P < 0.001$). This influence of wind declined with time (−0.020 ± 0.003, z = −5.893, $P < 0.001$) toward similar proportions as adults (Figure 4a). The probability for juvenile frigatebirds leaving with head winds was similar to adults (15.0%; z = −0.728, $P = 0.47$; Figure 2a) with no significant increase in time (z = 1.719, $P = 0.09$). Juvenile frigatebirds returned in a similar direction to their previous trip (within-individual consistency) in 26.0% of cases, which is more than expected by chance ($\chi^2 = 22.72$, df = 1, $P < 0.001$) but lower than adult behavior (−1.13 ± 0.14, z = −7.914, $P < 0.001$; Figure 2b). The probability of within-individual consistency in juveniles did not change with time (z = −0.093, $P = 0.93$). Finally, the probability of sharing similar directions for individuals leaving within the same time window (between-individual resemblance) was similar in juveniles as in adults (35.4%; $\chi^2 = 1.594$, df = 1, $P = 0.21$; Figure 2c) and slightly but significantly decreased in time (−0.0080 ± 0.0022, z = −3.646, $P < 0.001$). Conclusions were qualitatively unchanged when using different simultaneity thresholds (Supplementary Material S3).
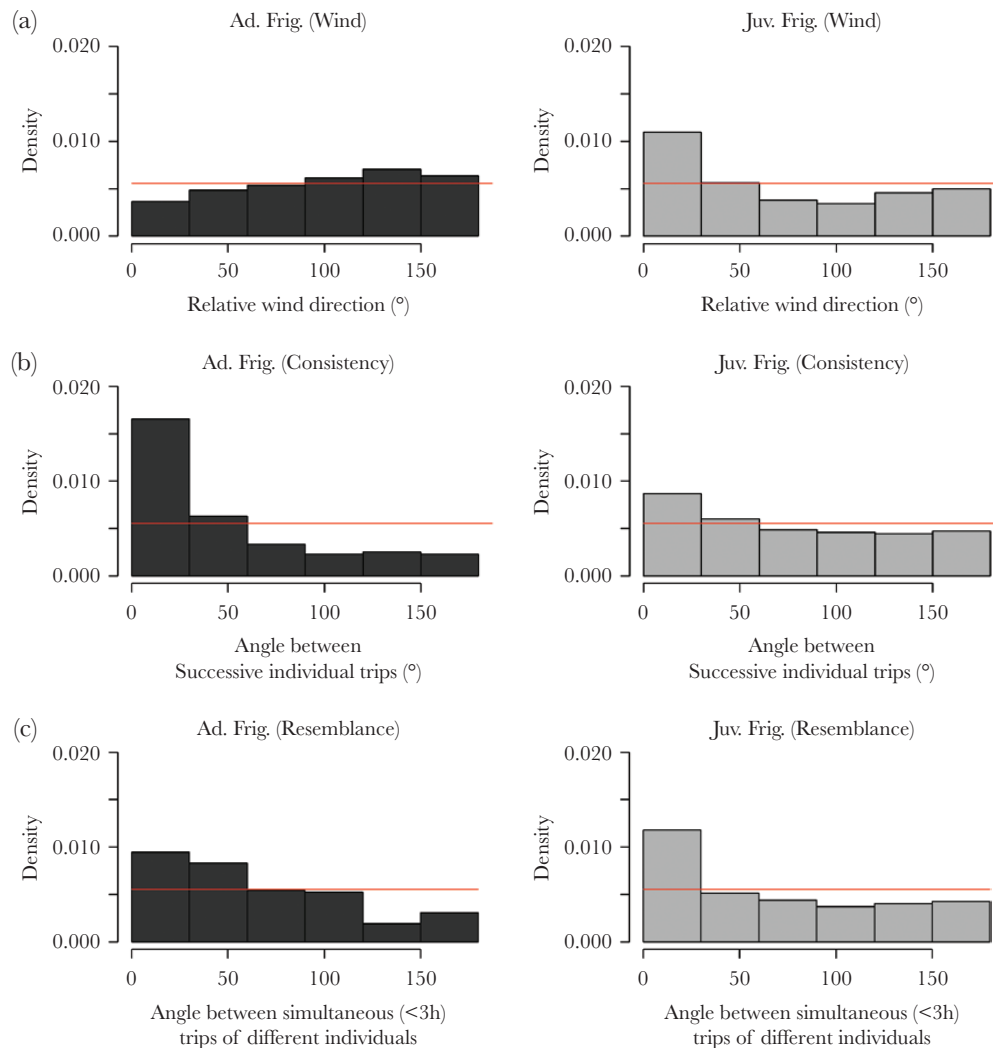
Figure 2
Influence on frigatebirds' trip directions of wind direction [(a) angle between wind direction and trip direction, i.e., 180° for front winds]; within-individual consistency [(b) angle between two successive trips by the same individual, i.e., 0° for identical directions]; and between-individual resemblance [(c) angle between trips of individuals leaving within 3 h of each other] in adults (left, dark gray) and juveniles (right, lighter gray). The probability density functions are used in *y* axis to scale histograms despite different sample sizes. Red lines materialize expected probabilities under the null hypothesis (uniform distribution: no privileged direction).

In juvenile red-footed boobies, the probability of leaving with tail winds increased with time (0.042 ± 0.019, $z = 2.203$, $P = 0.03$; Figure 4b) but was overall similar to adults (15.0%, $z = 0.381$, $P = 0.70$; Figure 3a). The use of front winds was similar in juvenile boobies as in adults (16.1%, $z = -0.359$, $P = 0.72$; Figure 3a), with no change through time (2014: $z = -0.311$, $P = 0.76$). Juvenile boobies returned to a similar direction as their previous trip (within-individual consistency) in 29.3% of cases, which is higher than expected by chance ($\chi^2 = 10.06$, df = 1, $P < 0.001$) but lower than in adults (-0.75 ± 0.32, $z = -2.368$, $P = 0.02$; Figure 3b). The probability of within-individual consistency did not change through time in juvenile boobies ($z = 0.108$, $P = 0.91$). The probability for juvenile boobies to share similar directions between individuals leaving within the same time window was similar to adults (between-individual resemblance: 31.5%, $\chi^2 = 0.639$, df = 1, $P = 0.42$; Figure 3c), with no progression through time ($z = 0.806$, $P = 0.42$). Conclusions were qualitatively unchanged when using different simultaneity thresholds (Supplementary Material S3).

Overall, juveniles of both species homed with less straight path than adults (frigatebirds: -0.17 ± 0.04, $t = -4.814$, df = 16, $P < 0.001$; boobies: -0.097 ± 0.029, $t = -3.400$, df = 25, $P < 0.01$; Figure 5a) and frigatebirds homed with lower average speeds than adults (frigatebirds: -6.9 ± 1.2 km/h, $t = -5.987$, df = 18, $P < 0.001$; boobies: $t = -1.268$, df = 31, $P = 0.21$; Figure 5b). We did not observe juvenile progression through time of homing straightness (frigatebirds: $t = -0.774$, df = 155, $P = 0.44$; boobies: $t = -0.231$, df = 8, $P = 0.82$) or homing speed (frigatebirds: $t = 1.780$, df = 159, $P = 0.08$; boobies: $t = 0.111$, df = 8, $P = 0.91$). All these modeling analyses incorporated wind direction and speed as covariates (Supplementary Material S3).

DISCUSSION

We examined in two sympatric species the foraging directions taken by newly fledged juveniles from the colony and their homing efficiency. We looked at how it changed through time and how it
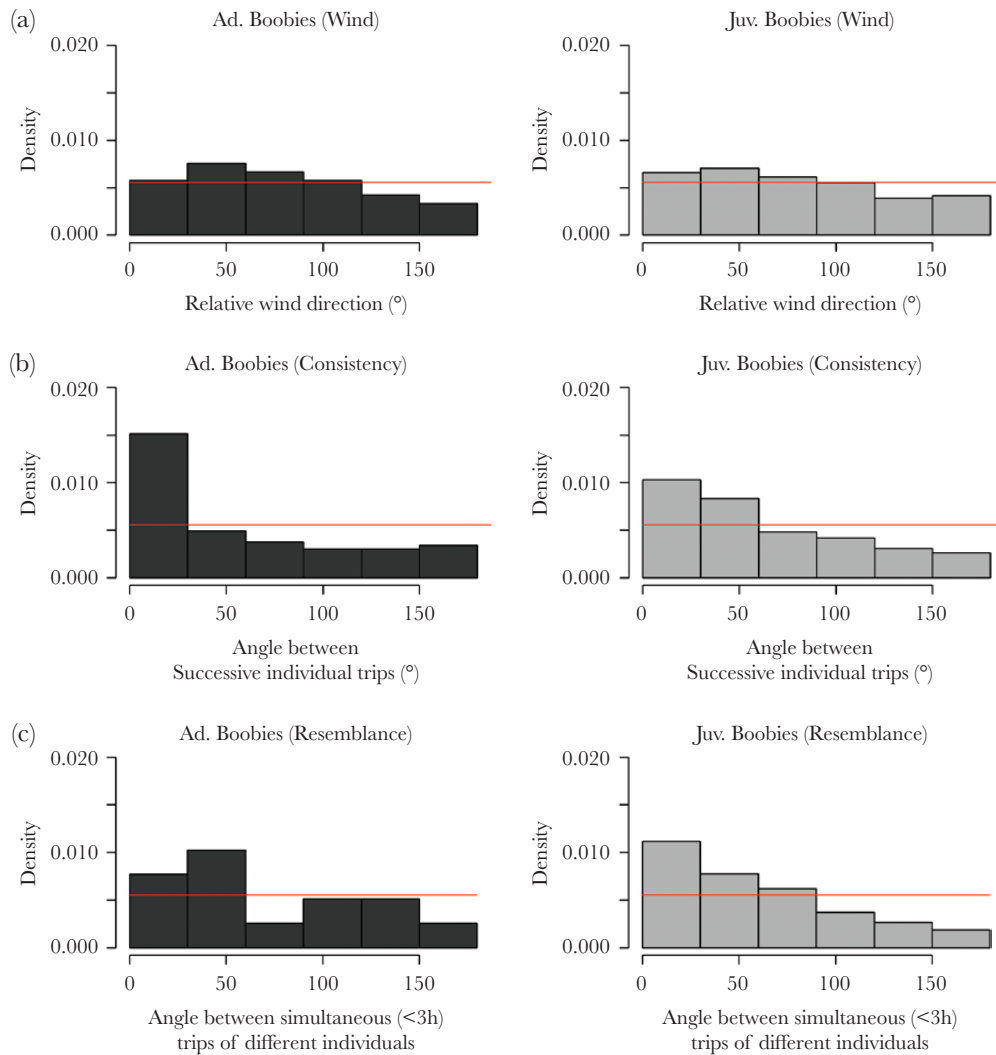
Figure 3

Influence on red-footed boobies' trip directions of wind direction [(a) angle between wind direction and trip direction, i.e., 180° for front winds]; within-individual consistency [(b) angle between two successive trips by the same individual, i.e., 0° for identical directions]; and between-individual resemblance [(c) angle between trips of individuals leaving within 3 h of each other] in adults (left, dark gray) and juveniles (right, light gray). The probability density functions are used in *y* axis to scale histograms despite different sample sizes. Red lines materialize expected probabilities under the null hypothesis (uniform distribution: no privileged direction).

compared with adult behavior (summary of predictions and results in Table 1). Overall, we found support for the early-exploration-later-canalization hypothesis rather than for the early-focus-later-generalization hypothesis. Our data supported the hypothesis that juveniles undergo a learning phase to overcome wind constraints on flight direction. This wind-related learning phase took weeks to months, but adult-like behavior was observed before independent dispersal. Moreover, this early wind influence was not strong enough to completely restrict decisions of foraging direction in young juveniles. In contrast, we did not find support for the early-conformism-later-self-defining hypothesis, nor for an anti-conformist strategy. Finally, we observed lower homing performances in juveniles even at the end of the study period, suggesting that navigation and/or flight skills still require a learning phase that could extend to the postdispersal phase.

The absence of support for the early-conformism-later-self-defining hypothesis may seem surprising. Indeed the strong wind constraints we observed on juvenile flight directions and

the apparent lower general efficiency in their homing behaviour and their flight (Yoda et al. 2004; Mendez et al. 2017; Yamamoto et al. 2017) suggest that juveniles are facing important costs and constraints in their first flights. It is often hypothesized that social learning could particularly help juveniles compensate for their lack of experience and the costs of individual trial-and-error (Kendal et al. 2005; Sherratt and Morand-Ferron 2018). It was previously shown from land-based observations that juvenile red-footed boobies often left the colony in small groups, returned in smaller groups or alone (Mendez et al. 2017), and GPS tracks anecdotally revealed close and dynamic associations at sea during foraging, although their prevalence could not be evaluated (Mendez et al. 2017). Here, we only had tracks on a limited number of individuals in the colony; social foraging and learning are likely to have occurred between tracked and nontracked individuals. However, at the population level, this would not have resulted in frequent and strong population-level instantaneous preferences for one or a few numbers of foraging directions (e.g.,
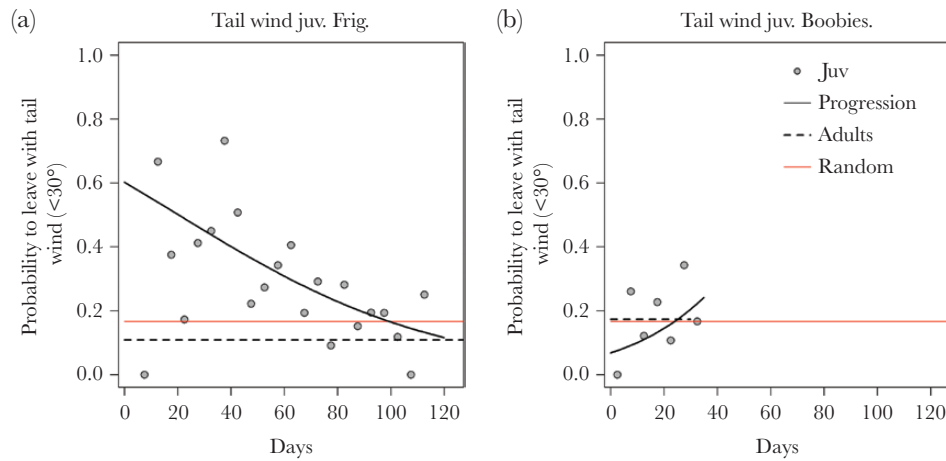
Figure 4
Juveniles' probability through time to leave the colony with tail winds (relative wind-trip direction <30°) in frigatebirds (a) and in red-footed boobies (b). Average values for adults of each species are shown by the dashed lines, random expectation (uniform distribution) is shown by the red solid line. Displayed probabilities (dots) are the proportions of respective angles <30° calculated by 5-day bins, but a continuous date variable was used for analyses.
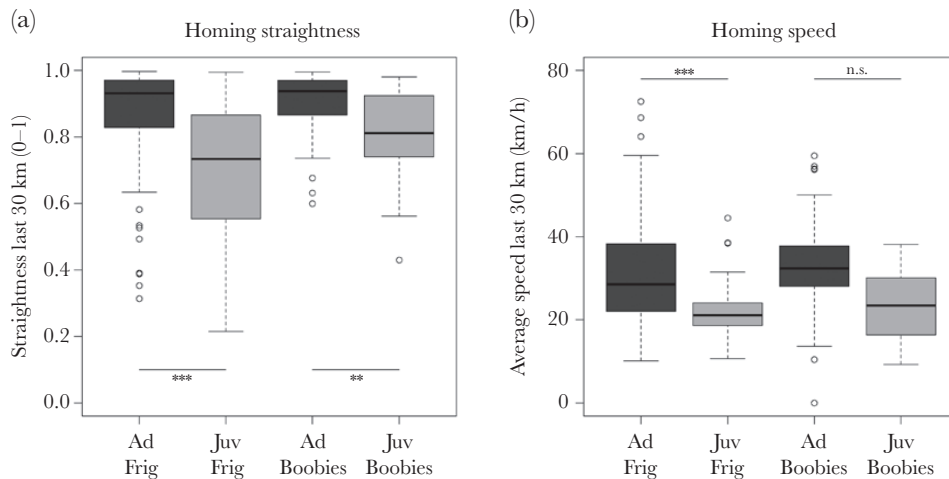

Figure 5
Homing capacities [(a) straightness; (b) average speed] of adults (darker gray) and juveniles (lighter gray) in both species; calculated for the portion of foraging trips from the last location >30 km from the colony to the colony.

Weimerskirch et al. 2010). These results imply, first, that there is an important initial interindividual variation in decision-making within these populations for natural selection to act on: leaving the same place at the same time does not trigger similar decisions among all juveniles. Second, individuals within these colonies would diverge very early in building their own individual experience, which could have important ecological and evolutionary implications (Mery 2013; Patrick and Weimerskirch 2014; Dukas 2017). On the other hand, the relatively low individual consistency in foraging direction suggests that juveniles are not specialized yet (see also Votier et al. 2017), which is perhaps not surprising given the apparent low adult specialization in tropical boobies and frigatebirds (Weimerskirch 2007; Ceia and Ramos 2015; Oppel, Beard, et al. 2015; Oppel et al. 2017). Overall, this early juvenile variability in space use and travel direction around the colony is also in contrast with their later dispersal behavior. Postfledging dispersion is often much more deterministic and oriented at the population level in many seabird species, including in the present

frigatebird population (Weimerskirch et al. 2006; De Grissac et al. 2016; Weimerskirch et al. 2016).

We found in both species that juveniles displayed some within-individual consistency in the successive trip direction as soon as their first trips. In the exploration-canalization hypothesis, young individuals start by widely exploring their environment and only later making better informed consistent decisions. The observed early tendency for individual consistency, although low, would slow down the spatial exploration by individuals and, therefore, seems at odds with the exploration-canalization hypothesis in its simplest formulation. This early individual consistency could allow juveniles to quickly experience the dynamic properties of their environment by comparing how conditions change across successive trips in a particular area at sea. Yet, it is unclear whether such an early experience would benefit survival through the subsequent immature phase because seabirds generally disperse hundreds to thousands of kilometers away from their natal areas for several years (De Grissac et al. 2016; Weimerskirch et al. 2016) and such knowledge of local

dynamics may not be transferable. Moreover, colonies often comprise nonbreeding adult-plumaged birds spending time around the colony, potentially including prebreeding immatures (Hamer et al. 2001; Nelson 2005), and individuals would, thus, have later opportunities to learn local environmental variability before reproduction (Votier et al. 2017). More data on this within-individual consistency tendency in different species and stages are required to better understand its determinants (Votier et al. 2017).

The main behavioral difference we found between the two species was in how juvenile foraging direction was influenced by wind. Frigatebirds have an extremely low wing loading for their size and use a very specific flight strategy relying on ascending air and gliding (Spear and Ainley 1997). They could be particularly sensitive to strong horizontal winds (Shepard and Lambertucci 2013), and naïve juveniles may require an initial learning or developmental phase to avoid being passively drifted by horizontal winds. This may be linked to the exceptionally long postfledging parental-care phase in this species (Nelson 2005; Corbeau et al. 2020). In contrast, the morphology of red-footed boobies, similar to that of albatrosses, seems more adapted for using horizontal wind to extract energy for dynamic soaring flight type (Ballance 1995; Weimerskirch et al. 2005). In wandering albatrosses, juveniles took several months to use wind like adults (Weimerskirch et al. 2006; Riotte-Lambert and Weimerskirch 2013). In particular, they tended to avoid tail winds in their first month at sea compared with older birds (Riotte-Lambert and Weimerskirch 2013), much similar to our results on juvenile boobies. At a finer scale, a recent study also showed how wind affected juvenile flight stability and energetics in the closely related brown booby (Yamamoto et al. 2017), and another one documented lower efficiency in thermal soaring in juvenile vultures compared with adults (Harel et al. 2016). Examination of wind use by juvenile birds, in general, is recent and available data are still limited (e.g., see review in Liechti 2006). Although we know that, in many migrating passerines and raptors, first-year individuals are able to head in a goal-oriented manner despite various wind directions (Liechti 2006), what happens in the period between fledging and migration is poorly documented, which we suggest is likely to depend on flight type and wing morphology.

The early juvenile variability (both low within-individual consistency and high between-individual differences) may be favored by the regular feeding by parents of their young fledgling who are not yet dependent on their own foraging efficiency (Nelson 1967; Nelson 2005; Guo et al. 2010). Testing this hypothesis would require to compare our results to other species with different lifestyles. The simple and straightforward methods we used here could easily be applied to a wide range of central place foragers, and comparisons can already be made with some previously published results. Spatial foraging specialization (i.e., a ratio of within-individual to between-individual resemblance) is often lower in seabirds when foraging constraints are lower (Oppel, Beard, et al. 2015; Votier et al. 2017). Our results also contrast with studies on the ontogeny of foraging flights in colonial wasps and bees of different species. After a few "exploration-orientation flights," hypothesized to mostly serve for learning homing cues and nest recognition (Degen et al. 2016; Mandal et al. 2017), foraging workers generally soon canalize into a few foraging spots to which they repeatedly return (Capaldi et al. 2000; Woodgate et al. 2016; Mandal et al. 2018). These rapid canalization strategies may be efficient for species with short life spans where the fitness of the colony relies on the efficiency of foragers (Raine and Chittka 2008). For instance, bumblebees foraged out of the colony for 6–15 days before dying (Woodgate et al. 2016).

In our long-lived species, more complex behavior may be at play: the foraging range and daily movement rates seem to increase more progressively (Baker 1993; Kohno and Yoda 2011; Riotte-Lambert and Weimerskirch 2013; Mendez et al. 2017); we did not observe analogs of the early "exploration-orientation flights" (Degen et al. 2015; Woodgate et al. 2016; Mandal et al. 2018); and, finally, seabird homing efficiency seems much slower to reach experienced adult levels. Here, it is unclear whether the lower homing efficiency of juveniles reflects different navigation mechanisms, different flight skills (Yoda et al. 2004), or even different behavioral motivations (Kohno and Yoda 2011; De Grissac et al. 2017; Mendez et al. 2017). However, the absence of progression in homing efficiency suggests that juveniles do not rely on learning landmarks at sea around the colony (Mandal et al. 2017). Hymenopterans differ from seabirds in many respects, and these comparisons are speculative, yet central place foraging should impose common constraints to very different organisms. Simple and widely applicable methods, such as the present one, could allow testing and discussing these comparisons to gain more biological insights into commonalities and differences between distant organisms.

In conclusion, our results fit with an early-exploration-later-canalization hypothesis (Votier et al. 2017), where adult individual consistency would not be expressed before dispersal by juvenile birds. The lower efficiency in homing, the shorter trips, and the initially strong influence of wind direction on trip direction in juveniles strongly suggest that these juveniles initially incur important costs and have to go through a learning phase of flight and/or navigational skills (Daunt et al. 2007; Riotte-Lambert and Weimerskirch 2013; De Grissac et al. 2016). We show that the importance and duration of this learning phase, at least in relation to wind conditions, may be largely dependent on species. However, the lack of evidence for a decrease in between-individual differences in postfledging juveniles compared with adults, and the absence of progression in juvenile direction decision-making and homing behavior, can also suggest an alternative nonmutually exclusive hypothesis. Rather than reflecting a purely developmental phase, part of the differences observed between juveniles and breeding adults may come from the asymmetric foraging constraints: parents are highly constrained on their foraging efficiency to feed both themselves and their chick, whereas juveniles are fed daily by their parents (Nelson 2005). Such a relaxation on the efficiency of self-feeding may allow juveniles to be more exploratory. This could also explain why failed adult breeders can show much less individual site consistency than breeding adults (Votier et al. 2017), as well as the apparently much quicker development of individual site consistency in naïve hymenopterans foraging around the colony (Raine and Chittka 2008; Woodgate et al. 2016; Mandal et al. 2018). Hymenopterans may provide interesting systems in which to further test these alternative hypotheses through natural-experimental manipulations.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by (Collet et al. 2020).

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