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Navigating the unknown: how exploratory traits shape juvenile post-fledging behaviour and survival in gulls.

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The post-fledging period is a critical phase for inexperienced birds, who must navigate and explore unfamiliar environments to locate essential resources for survival. Successful foraging during this stage relies on acquiring spatial knowledge through exploration, which may develop early in life. In this study, we examined whether the early-life exploratory phenotype, assessed through an open field test (OFT) during the nestling phase, predicts post-fledging behaviour and survival. GPS tracking data from 34 juvenile lesser black-backed gulls (*Larus fuscus*) over a 20-day period were used to quantify habitat preferences, spatial use (mean squared displacement and revisitation patterns) and time spent flying, foraging and resting. Survival was monitored over six months following fledging, encompassing migration. Early-life exploratory phenotype predicted habitat use: individuals with a more exploratory phenotype frequented urban habitats more often, whereas those with a less exploratory phenotype relied more on agricultural areas. However, exploratory phenotypes did not predict spatial use or survival. These findings indicate that behavioural variation established early in life can have lasting ecological consequences. The absence of a link between exploratory phenotype and survival may reflect phenotype-habitat matching, stochastic environmental factors, or that the OFT does not capture the behavioural components most relevant to survival.

1. Introduction

The transition to independence marks a critical phase in the lives of many animals. As juveniles must navigate unfamiliar environments, locate resources and avoid threats without prior experience, this stage is typically associated with high mortality [1–3]. Exploration, broadly defined as the acquisition of information through movement and interaction (e.g. [4,5]), is central to overcoming these challenges. It enables individuals to identify profitable foraging areas, suitable locations for shelter or rest and alternative habitats that may buffer against environmental fluctuations [5–10]. However, exploration also entails time, energetic, opportunity and predation costs [5], and its fitness value is highly context-dependent. For instance, while exploration can improve foraging success under resource unpredictability, it may increase mortality when risk avoidance is predominant [11].

Such fluctuating selection pressures are thought to maintain the broad variation in exploratory phenotypes observed within and among species [12]. Even within populations, individuals differ consistently in their motivation to explore novel environments [13,14], and these differences have been linked to other behavioural and cognitive traits such as boldness and learning ability [15,16]. Such consistent differences may also have important ecological implications. For instance, starlings (*Sturnus vulgaris*) that explore larger areas in captivity later maintain broader home ranges in the wild [17], suggesting that exploration can influence how individuals interact with and learn about their environment.

Despite extensive research on exploration in birds, little is known about how early life differences in exploratory behaviour translate into later movement and survival outcomes. This gap partly reflects the logistical difficulty of measuring behaviour before independence. As a result, most studies assessed exploration only after fledging, when selective mortality may have already filtered out certain behavioural types, potentially obscuring causal links between early traits and later performance. A few recent studies begin to bridge this gap. Rotics *et al.* [18] investigated post-fledging exploration and dispersal in white storks (*Ciconia ciconia*), finding that individuals that moved more extensively after fledging had higher first-year survival. They also quantified pre-fledging activity levels, which predicted these later outcomes, but this measure captured general movement propensity rather than standardized exploratory motivation. Similarly, Portugal *et al.* [19] demonstrated that exploration of novel objects in young homing pigeons (*Columba livia*) predicted subsequent flight range and homing efficiency, but their tests were conducted post-independence. Both studies suggest important developmental links between early behaviour and later outcomes, but have not directly connected experimentally measured exploratory phenotype before fledging with post-fledging space use and survival in the wild.

Semi-precocial species, such as many colonial seabirds, offer unique opportunities to quantify early behavioural phenotypes before independence. Their chicks are mobile and interactive well before fledging but remain accessible for standardized behavioural testing within the colony environment. This developmental strategy allows the use of standardized behavioural assays, such as the open field test (OFT), which is commonly applied to assess exploratory behaviour in controlled settings and link it to performance in the wild (e.g. [14,20–22]). The lesser black-backed gull (*Larus fuscus*) is particularly well suited for this approach: it breeds colonially, its chicks exhibit clear and repeatable behavioural differences during development, and individuals can be tracked after fledging using lightweight GPS devices. A previous study on this population used the OFT to quantify exploratory behaviour at 20 ± 5 days of age (before juveniles were exposed to the broader ecological and social challenges post-independence) and found that the early social environment shapes individual differences in exploratory phenotype [23]. Building on this work, we test whether early-life exploratory phenotype predicts multiple dimensions of post-fledging behaviour during the critical transition to independence.

For this study, a subset of the individuals tested by Salas *et al.* [23] were equipped with GPS tags for post-fledging tracking. To examine how their pre-fledging exploratory phenotype, quantified through the OFT, relates to post-fledging behaviour, we analysed multiple movement metrics describing how individuals navigate and interact with novel environments after independence. First, we assessed flight activity, the extent to which juveniles showed localized versus wide-ranging movements, and their revisitation patterns, predicting that more exploratory individuals would spend more time flying, exhibit broader space use as reflected in higher mean squared displacement (MSD) and revisit specific locations less frequently [17,24–26]. Second, we analysed the diversity and complexity of habitats used (marine, urban, agricultural), expecting that exploratory individuals would either exploit a wider range of habitats or preferentially use complex, resource-rich environments such as urban areas [27,28]. Consistent with the latter idea, urban-adapted birds are typically more exploratory than their rural counterparts [28–30], although the causal direction (i.e. environmental influence versus behavioural self-sorting) remains unresolved. To assess the potential functional significance of both pre- and post-fledging variation, we then examined whether exploratory phenotypes were associated with differences in survival during the critical six-month period post-fledging. While enhanced spatial knowledge and behavioural flexibility may offer important advantages during this life stage, these benefits may be weighed against the costs of exploration.

2. Material and methods

(a) Study area and pre-fledging measurements

In 2020 and 2021, the nests of lesser black-backed gulls (108 nests in 2020 and 78 in 2021) were monitored three times a week from the end of April in the harbour colony of Zeebrugge (Belgium, $51^{\circ}20'N$, $3^{\circ}10'E$), containing approximately 300 breeding pairs. This fenced colony is characterized by an artificial, sparsely vegetated and sandy environment. The laying dates of all eggs were recorded, and the chicks were individually labelled at the first control after hatching to ensure an accurate determination of chick origin and age. In addition, down feathers were collected at hatching for molecular sex determination using PCR [31]. At fledging (age $30 (\pm 2)$ days), body mass (g), tarsus length (mm), head size (mm) and wing length (mm) were measured, from which a scaled body mass was calculated using body mass and tarsus length according to [32].

(b) Open field test (OFT) and principal component analysis

Pre-fledging exploratory phenotype, as defined in §1, was measured using the OFT. The test was conducted in a 3×3 m arena located next to the colony, on individuals aged 20 ± 5 days (for a full description, see [23]). The arena setup included a concrete block, representing a familiar shelter (i.e. similar to those present next to each nest in the colony) and a 1×1 m red carpet placed at the centre of the arena, which served as a novel object. After a brief acclimatization period, individuals were released into

the arena and their behaviour was filmed for 10 min. The latency to enter the shelter, the time spent in the shelter, the latency to cross the novel object, the time spent on the novel object and the time spent moving and exploring were recorded. A total of 90 chicks performed this test (46 in 2020 and 44 in 2021); all chicks were unrelated as only one individual per nest (usually the first-hatched chick) was tested (further details can be found in [23]).

A principal component analysis (PCA) was conducted on the behavioural variables to reduce dimensionality and identify underlying behavioural axes (see [23]). The analysis yielded two main axes (see additional file, electronic supplementary material, table S3). The first axis, which explained 37% of the variance, was associated with exploratory behaviours, being positively related to time spent moving and carpet use duration, and negatively related to latency to cross the carpet. It was therefore the focus of the present study. Lower scores on this axis correspond to a higher early exploratory phenotype. The second axis, which explained 41% of the variance, reflected anxiety-related behaviours (shelter use duration and latency to shelter) and was not considered further in the main analyses (see additional file, electronic supplementary material, tables S4–S7).

(c) GPS tracking

From the chicks tested in the OFT by Salas *et al.* [23], 51 unrelated individuals were fitted at fledging with solar-powered Ornitela OT-15-3G GPS devices using Teflon ribbon wing harnesses designed to prevent injuries and ensure unrestricted movements [33]. Only juveniles weighing at least 600 g were equipped, ensuring that the combined weight of the tracker and harness did not exceed the ethical threshold of 2.5% of the body mass, as recommended [33,34] (see additional file, electronic supplementary material, table S1). Devices were fitted and adjusted under ethical approval by experienced handlers, allowing the procedure to be efficient and to cause minimal stress to the birds (see details of the GPS-tagging procedure in additional file, electronic supplementary method).

Most GPS trackers were configured to record locations every 20 min. A few trackers operated at a higher sampling frequency but were subsequently subsampled to a 20 min resolution to avoid sampling bias. In 2020, predation by local foxes resulted in the immediate loss of at least ten tagged gulls after they left the fenced part of the colony. To prevent similar losses, juveniles in 2021 were temporarily transferred to a secure aviary in Ostend for 5 weeks before being tagged and released on an estuarine beach approximately 30 km from their natal colony [35].

(d) GPS data processing

The GPS data of the 51 birds were pre-processed in R [36] (v. 4.3.3), as described in [35]. First, we enriched the GPS data with land-use information sourced from the Moderate Resolution Imaging Spectroradiometer (MODIS 500 m type1) available in the NASA database [37]. These data were categorized into three habitat types: agricultural, marine and urban. Agricultural habitats included ‘savannas’ (i.e. tree cover 10–30%), ‘grasslands’ (i.e. dominated by herbaceous annuals (<2 m)), ‘croplands’ (i.e. at least 60% of area is a cultivated cropland) and ‘cropland/natural vegetation mosaics’ (i.e. mosaics of small-cultivation 40–60% with natural tree, shrub or herbaceous vegetation). Marine habitat corresponded to ‘water bodies’ (i.e. at least 60% of area covered by permanent water bodies). Urban habitat corresponded to ‘urban/built-up lands’ (i.e. at least 30% impervious surface area including building materials, asphalt and vehicles).

Behavioural categories (‘foraging’, ‘flying’ or ‘resting’) were assigned to each GPS fix using a random forest classifier [38]. The model used a combination of parameters, including ground speed, turning angle, step length and MODIS land-use data. The classifier was trained and validated on expert-annotated data and optimized using multiple input streams, achieving high accuracy (83.2%) in distinguishing behaviours.

For both years, GPS fixes were retained only for a 20-day period starting from the 21st of August, which corresponded to the release date of the juveniles in 2021 and was matched for the juveniles of 2020 to minimize seasonal differences. A 20-day time frame was chosen to ensure comparability among individuals before the onset of migration, which can affect flight-related measures and increase variance owing to differences in habitat availability, while also maintaining consistency with previous work on this population [35]. The 13 birds that did not survive until the end of this 20-day period were excluded, as well as the three individuals with data gaps exceeding 12 h. Additionally, to avoid the influence of sick individuals or individuals in poor body condition that may have exhibited abnormal behaviour, we verified that the birds survived at least 5 days beyond the end of the study period. All individuals met this criterion and were therefore retained at this step. Finally, based on visual inspection, we excluded one individual that migrated directly to Spain during the study period, which represented an outlier in the context of spatial metrics when compared with the other juveniles. Ultimately, 34 juveniles (16 females and 18 males) were included in the analyses (additional file electronic supplementary material, figure S1). However, for the analysis of the effect of early-life exploratory phenotype on habitat use, habitat use diversity and foraging effort, a further four individuals were excluded because they spent less than 7% of their time foraging (see additional file, electronic supplementary material table S2 and figure S2), suggesting that they were probably still being fed by their parents.

To assess how juveniles use the different habitats, we calculated the proportional use of agricultural, marine and urban habitats, quantified as the ratio of GPS fixes within each habitat to the total number of GPS fixes collected during daylight hours [35]. We also calculated a coefficient of evenness to determine the diversity of habitats used by each individual, using the formula:

$\frac{1}{\sum_{\text{habitat types}} \text{habitat proportions}^2}$, from Simpson’s Evenness Index [39]. Then, this coefficient was normalized between 0 and 1 by applying the following formula: $\frac{(\text{coefficient of individual } x - \text{minimum coefficient})}{(\text{maximum coefficient} - \text{minimum coefficient})}$. A coefficient of 0 expressed the exclusive use of a single habitat.

To assess spatial use and reuse over the first 20 days after the start of the study period, we calculated MSD (in square metres), using the `msd()` function of the package 'amt' (v. 0.2.1.0) [40] and the total number of revisits, using the `getRecursions()` function of the 'recurse' package (v. 1.1.2) [41]. MSD summarizes the spatial use of individuals and is especially useful in this study where juveniles do not have an established home range [42]. MSD is tightly linked with structural elements of the track, such as tortuosity, and conversely, straightness [42,43]. We do not interpret absolute MSD values in isolation, as recommended by [42]. Instead, we use MSD to compare space use among individuals. Relatively lower MSD values indicate more localized, encamped movements, suggesting that a bird stays within a smaller and probably more familiar area. By contrast, relatively higher MSD values reflect diffusive, non-oriented movements, indicating that the bird covers a larger area and may be venturing into new environments. Thereafter, a 5 km buffer was applied to each GPS location. After the initial departure from an area, subsequent revisits, defined as GPS fixes falling within the same buffer, were counted and summed per individual. The number of revisits was then used as a measure of preference for particular areas (e.g. roosts, foraging sites or resting areas; [44]). The 5 km radius was chosen here to capture spatial reuse of familiar foraging areas at an ecologically relevant scale, representing only a small fraction of the typical daily movement range of juvenile lesser black-backed gulls (approx. 40 km; [35]).

Finally, we quantified the relative frequency of the classified behaviours: flying, foraging and resting, as measures of foraging effort, by calculating the ratio of GPS fixes annotated with each behaviour to the total number of GPS fixes during the day [35].

(e) Inference of mortality from tracking data

When possible, carcass recovery and tag retrieval were used to confirm mortality. However, for most individuals, death had to be inferred from tracking data. We identified mortality based on tri-axial accelerometer and GPS movement data. For each individual, we examined time series of the magnitude of acceleration, as well as GPS-derived step lengths. A flatline in acceleration, indicative of minimal or absent body movement, for at least 48 consecutive hours while the tag continued transmitting, was used as an operational indicator of death. Limited movements (≈ 30 m between successive GPS fixes, corresponding to device precision) over at least 48 h were used as an additional indicator of death. Accordingly, individuals were classified into three categories: (i) alive, when regular acceleration and movements persisted until the end of the study period; (ii) dead, when clear acceleration flatlining and absence of movement were observed, or when carcass and GPS tag were recovered; and (iii) uncertain, when GPS transmission stopped abruptly while acceleration and movement data prior to the last fix showed normal activity, suggesting possible tag malfunction.

(f) Statistical analysis

(i) Movement analysis

In all models, we used each individual's score on the exploratory axis from the OFT PCA as their early exploratory phenotype score (more negative values indicate a higher exploratory phenotype). All models also included the scaled body mass, sex and year of tagging as covariates. Sex and year were treated as factors in the models. Early exploratory phenotype scores and scaled body mass were scaled and centred using the `scale()` function. Models were fitted using the 'lme4' (v. 1.1-34) [45], 'lmerTest' (v. 3.1-3) [46] and 'glmmTMB' (v. 1.1.7) [47] packages in R. An alpha level of 0.05 was used to determine statistical significance. Model fits and residuals were evaluated using the 'performance' (v. 0.10.4) [48] and 'DHARMA' (v. 0.4.6) [49] packages. Data visualization was performed using 'ggplot2' (v. 3.4.3) [50].

To evaluate the effects of the early exploratory phenotype on habitat use post-fledging, we fitted three general linear models (GLM) with a beta distribution to the proportions of agricultural, marine and urban habitat use, using the `glmmTMB()` function. To examine the effects of early exploratory phenotype on diversity in habitat use, we fitted a linear model (LM) with Gaussian distribution to the coefficient of evenness.

To estimate the influence of the early exploratory phenotype on space use and space reuse post-fledging, we fitted two LMs with Gaussian distribution using the log-transformed MSD, and the number of revisits (untransformed) over the study period, as response variables in the two models, respectively.

Finally, we assessed the impact of the early exploratory phenotype on foraging effort post-fledging by fitting three LMs with Gaussian distributions to the proportions of foraging, flying and resting behaviours, thereby assessing time allocation between different behavioural activities [35].

(ii) Survival analysis

In the survival analyses, deaths were coded as events ($\text{status} = 1$). Individuals classified as alive at the end of the 6-month monitoring period, as well as those classified as uncertain, were treated as right-censored ($\text{status} = 0$). Censoring occurred at the individual-specific time of the last GPS fix. Thus, birds known to be alive were censored at 180 days, whereas uncertain individuals were censored earlier, at the date when GPS transmission ceased. This approach, using Cox proportional hazard (CPH) analyses, allowed uncertainty in individual fate to be incorporated conservatively without making assumptions about the true survival time of individuals whose tags failed.

We tested whether early exploratory phenotype correlates with the survival probabilities during the high-risk post-fledging period [51]. In fact, more than half of the juveniles died within the first 6 months after tagging (29 out of 51 individuals), a time during which the species faces the challenges of migration. We conducted a multivariate CPH analysis using the `coxph()` function from the 'survival' R package (v. 3.5-8) [52], modelling the effect of multiple predictors on survival time, measured as

the number of days that each individual lived over the 6-month sampling period. The model included pre-fledging exploration score as explanatory variable and scaled body mass at tagging, sex and year of tagging as covariates.

Next, we assessed whether post-fledging habitat use, spatial (re)use and foraging effort were associated with juvenile survival over the 6+month period, using a CPH model. After checking for multicollinearity using the `vif()` function from 'car' package (v. 3.1-2) [53], we included MSD, habitat diversity (coefficient of evenness), number of revisits and the proportion of time spent foraging as predictors. Sex, year of tagging and scaled body mass at tagging were again included as covariates.

In these models, a positive regression coefficient indicates a higher risk of mortality, and the hazard ratio represents the change in mortality probability associated with a one-unit increase in the predictor [18]. The proportional hazard assumptions were verified using scaled Schoenfeld residuals with the `cox.zph()` function from the 'survival' package [52] and residual plots were visually inspected to assess model fit.

3. Results

(a) Habitat use, spatial (re)use and foraging effort

The early exploratory phenotype score was negatively correlated with the extent of urban habitat use, indicating that juveniles displaying higher exploratory behaviour during the OFT used urban habitats more frequently; conversely, juveniles that were less exploratory used agricultural habitat more frequently (table 1, figure 1A,B). In addition, birds with a higher scaled body mass index used marine habitat more frequently, while juveniles with a lower scaled body mass index exploited urban habitats more frequently (table 1). The early exploratory phenotype did not significantly influence habitat use diversity (table 1; additional file, electronic supplementary material, figure S3).

No significant effect of the early exploratory phenotype was found on MSD (table 2; additional file, electronic supplementary material, figure S4.A). However, spatial use differed between sexes, with females exhibiting larger MSD than males (table 2). The early exploratory phenotype had no significant effect on the number of times that juveniles revisited locations (table 2; additional file, electronic supplementary material, figure S4.B).

Finally, the early exploratory phenotype did not significantly correlate with the proportions of foraging, flying and resting (table 3; additional file, electronic supplementary material, figure S5). Females were flying proportionally more often than males (table 3; additional file electronic supplementary material, figure S6).

(b) Survival analysis

A total of 29 individuals died during the 6 months following fledging. Causes of death could be determined reliably for only a small proportion of these birds, and for these, most early deaths were probably owing to predation or traffic collisions. The early exploratory phenotype was not significantly associated with survival over 6 months following tagging (table 4). We also did not find a significant correlation between post-fledging habitat use, space (re)use, foraging effort and survival (table 5; additional file, electronic supplementary material, figure S16).

4. Discussion

This study examined whether the early-life exploratory phenotype, assessed in an OFT, predicts multiple dimensions of post-fledging behaviour in juvenile lesser black-backed gulls, including spatial movement patterns, habitat use and survival. We only found effects for habitat use: individuals that were more exploratory before fledging made greater use of urban habitats after fledging, whereas less exploratory individuals used agricultural areas more frequently. This pattern suggests a possible phenotype–habitat matching (or niche-picking) process, whereby individuals select environments that best fit their behavioural tendencies. Such matching could in turn explain why early exploratory behaviour was not directly related to survival if different habitats offer comparable overall fitness outcomes for different behavioural types.

(a) Early exploratory phenotypes shape habitat but not spatial use patterns post-fledging

First, aligned with our expectations, we found that individuals with a more exploratory pre-fledging phenotype foraged more frequently in urban habitats after fledging, which in our analysis encompassed industrial areas, built-up zones and city centres. Urban environments exhibit spatial heterogeneity [27,54] and the patchy distribution of the anthropogenic resources in both time and space may initially demand greater exploration to locate and assess them. Previous studies have reported similar associations between exploratory phenotypes and urban habitat use in adult birds [27,28,30,55]. For example, Thompson *et al.* [56] found that black-capped chickadees (*Poecile atricapillus*) caught in urban habitats explored novel environments faster than rural birds. However, in most of the previous studies, the exploratory phenotype was always assessed after independence. Consequently, it could not be determined whether behavioural traits shaped habitat use or *vice versa*. By contrast, our study identified an individual's exploratory phenotypes before fledging, providing stronger evidence that early-life behavioural traits, such as exploratory behaviour, influence subsequent urban habitat selection.

Second, juveniles with a lower exploratory phenotype used agricultural habitats more frequently after fledging. Agricultural habitats—typically large and uniform pastures or crop fields—are characterized by high environmental homogeneity.

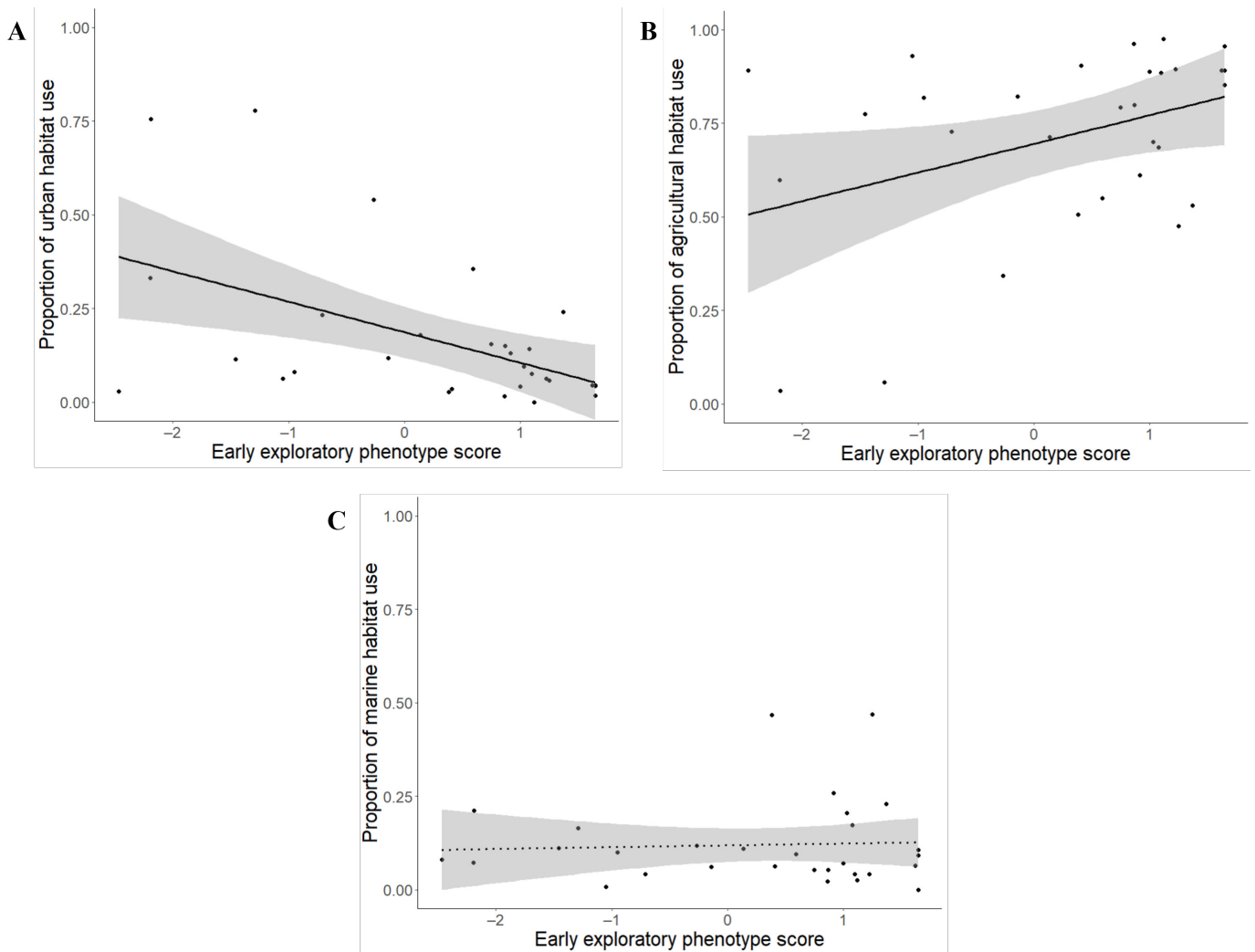


Figure 1. Relationships between the early exploratory phenotype score measured during open field test before fledging and the proportions of (A) urban habitat use, (B) agricultural habitat use and (C) marine habitat use post-fledging. The grey areas correspond to the standard error.

Such environments provide relatively uncompetitive foraging opportunities that require little exploratory effort because food availability is easily signalled by agricultural activities and the presence of conspecifics [57,58].

Third, we found no relationship between exploratory phenotype and the use of marine habitats, which may partly reflect the fact that this habitat type was used least frequently. This contrasts with a recent study on juveniles of the closely related yellow-legged gulls (*Larus michahellis*), which reported preferential foraging in ports and at sea [59]. However, our results align with the habitat preferences of adult lesser black-backed gulls during the same period [35,60].

Contrary to our predictions, individuals with a more exploratory phenotype did not fly more, show broader space use (MSD), or revisit specific locations less often. This absence of significant effects is intriguing but may be explained by their greater use of urban habitats, where animals often travel shorter distances and occupy smaller ranges [61]. Such patterns probably reflect the high concentration of resources in urban environments, which reduces the need for extensive movement. Similar trends have been observed, for example, in raccoons (*Procyon lotor*), where urban individuals maintained more restricted home ranges than their rural counterparts [62]. Urban exploration in lesser black-backed gulls may also involve more localized or opportunistic foraging strategies [63], further reducing overall movement in resource-dense environments. Another, not mutually exclusive, explanation is that differences among exploratory phenotypes in spatial movement may only emerge later in development. Early after fledging, all juveniles must explore to some extent to acquire information about their surroundings, and this shared need for environmental sampling may initially mask individual variation. As experience accumulates and foraging routines become established, exploratory phenotypes may then begin to produce more divergent spatial behaviours. We could not test this possibility here, as our analyses focused on the first 20 days post-fledging, before such developmental differences are likely to become apparent. A longer analytical window was not feasible because rapid loss owing to mortality, tag loss (and reduced performance of solar-powered devices later in the season) and large-scale migration resulted in insufficient statistical power for robust longer-term analyses. Dedicated follow-up studies with larger long-term samples will therefore be needed to evaluate whether early exploratory phenotype and juvenile habitat use predict later spatial behaviour, habitat use and migratory destinations.

It is important to note that the OFT provides a standardized and controlled measure of exploratory phenotype rather than a direct analogue of exploration in natural settings [12,17,64–66]. The test is designed to quantify individual differences in the motivation to move and interact within a novel environment. While OFT-derived measures may also capture elements of other behavioural traits, such as shyness, boldness or anxiety [67], they nonetheless provide meaningful information about

Table 1. Results of regression analyses testing whether the early exploratory phenotype predicts habitat use and habitat use diversity over the first 20 days following the start of the study period ($n = 30$ juveniles). Note that the early exploratory phenotype score is based on a PCA, where more negative scores indicate higher exploratory phenotype. Covariates are shown in *italics*, significant relationships are shown in **bold**.

	estimate \pm s.e.	<i>p</i> -value
1. Proportion of urban habitat use		
intercept	-1.17 \pm 0.43	0.007
early exploratory phenotype	-0.43 \pm 0.19	0.025
scaled body mass	-0.35 \pm 0.17	0.042
<i>sex</i>	-0.66 \pm 0.39	0.090
<i>year of tagging</i>	-0.28 \pm 0.43	0.513
2. Proportion of agricultural habitat use		
intercept	0.25 \pm 0.41	0.545
early exploratory phenotype	0.42 \pm 0.18	0.020
<i>scaled body mass</i>	-0.05 \pm 0.18	0.758
<i>sex</i>	0.56 \pm 0.38	0.139
<i>year of tagging</i>	0.36 \pm 0.42	0.388
3. Proportion of marine habitat use		
intercept	-2.43 \pm 0.40	<0.001
early exploratory phenotype	-0.29 \pm 0.16	0.064
scaled body mass	0.43 \pm 0.18	0.016
<i>sex</i>	0.11 \pm 0.37	0.766
<i>year of tagging</i>	0.47 \pm 0.39	0.226
4. Coefficient of evenness		
intercept	0.44 \pm 0.13	0.002
early exploratory phenotype	-0.03 \pm 0.06	0.576
<i>scaled body mass</i>	0.08 \pm 0.06	0.169
<i>sex</i>	-0.06 \pm 0.11	0.629
<i>year of tagging</i>	-0.02 \pm 0.13	0.891

Table 2. Results of regression analyses testing whether the early exploratory phenotype predicts spatial (re)use over the first 20 days following the start of the study period ($n = 34$ juveniles). Note that the early exploratory phenotype score is based on a PCA, where a more negative score indicates a higher exploratory phenotype. Covariates are shown in *italics*, significant relationships are shown in **bold**.

	estimate \pm s.e.	<i>p</i> -value
1. Mean squared displacement (m ²)		
intercept	16.35 \pm 1.27	<0.001
early exploratory phenotype	0.03 \pm 0.60	0.954
<i>scaled body mass</i>	0.27 \pm 0.64	0.679
sex	2.54 \pm 1.22	0.046
<i>year of tagging</i>	2.31 \pm 1.29	0.083
2. Number of revisits		
intercept	41.37 \pm 10.47	<0.001
early exploratory phenotype	-0.32 \pm 4.94	0.948
<i>scaled body mass</i>	-7.63 \pm 5.27	0.158
<i>sex</i>	-5.97 \pm 10.04	0.556
<i>year of tagging</i>	-6.13 \pm 10.62	0.568

how individuals respond to novelty. In our study, we used a PCA to distinguish between different behavioural components. Furthermore, the behaviours contributing to the exploratory axis, particularly the time spent on the red carpet and the latency to reach it, reflect investigation rather than escape attempts, supporting their interpretation as indicators of exploration rather than, e.g. anxiety. Arguably, because our version of the OFT primarily captured the motivational aspects of responding to

Table 3. Results of regression analyses testing the relationship between the early exploratory phenotype and foraging effort over the first 20 days following the start of the study period ($n = 30$ juveniles). Note that the early exploratory phenotype score is based on a PCA, where a more negative score indicates a higher exploratory phenotype. Covariates are shown in *italics*, significant relationships are shown in **bold**.

	estimate \pm s.e.	<i>p</i> -value
1. Proportion of foraging		
intercept	0.50 \pm 0.09	<0.001
early exploratory phenotype	0.07 \pm 0.04	0.089
<i>scaled body mass</i>	-0.03 \pm 0.04	0.487
<i>sex</i>	0.07 \pm 0.08	0.380
<i>year of tagging</i>	0.09 \pm 0.09	0.314
2. Proportion of flying		
intercept	0.10 \pm 0.02	<0.001
early exploratory phenotype	0.007 \pm 0.009	0.439
<i>scaled body mass</i>	0.01 \pm 0.009	0.277
sex	0.05 \pm 0.02	0.018
<i>year of tagging</i>	-0.007 \pm 0.02	0.730
3. Proportion of resting		
intercept	-1.21 \pm 0.33	0.001
early exploratory phenotype	-0.22 \pm 0.14	0.126
<i>scaled body mass</i>	0.07 \pm 0.14	0.612
<i>sex</i>	-0.30 \pm 0.29	0.299
<i>year of tagging</i>	-0.19 \pm 0.32	0.555

Table 4. Results of a CPH model analysing the relation between the early exploratory phenotype and survival post-fledging ($n = 51$ juveniles). A positive regression coefficient reflects an increase in the probability of mortality with this predictor. Covariates are shown in *italics*, significant relationships are shown in **bold**.

	β coefficient	s.e.	HR	<i>z</i>	<i>p</i> -value
early exploratory phenotype	-0.13	0.21	0.88	-0.61	0.540
<i>scaled body mass</i>	-0.03	0.22	0.97	-0.15	0.878
<i>sex</i>	-0.43	0.40	0.65	-1.09	0.277
<i>year</i>	-0.01	0.44	0.99	-0.03	0.978

Table 5. Results of a CPH model analysing the relation between post-fledging exploratory metrics and survival over a 6 months period post-fledging ($n = 34$ juveniles). A positive regression coefficient reflects an increase of the probability of mortality with this predictor. Covariates are shown in *italics*.

	β coefficient	s.e.	HR	<i>z</i>	<i>p</i> -value
mean squared displacement	-0.26	0.33	0.78	-0.77	0.440
coefficient of evenness	-0.63	1.23	0.53	-0.51	0.611
number of revisits	-0.003	0.009	1.00	-0.35	0.730
proportion of foraging	-3.07	1.88	0.05	-1.64	0.102
<i>sex</i>	-0.56	0.68	0.57	-0.83	0.407
<i>year</i>	1.74	1.30	5.68	1.34	0.181
<i>scaled body mass</i>	0.03	0.38	1.03	0.08	0.940

novelty rather than the spatial extent of movement, it may be better suited to predicting where individuals choose to forage (habitat use) than how widely they move across the landscape (spatial use).

(b) When context matters: constraints on the predictive power of early exploratory phenotype

An individual's exploratory phenotype is only one of multiple factors that may influence post-fledging behaviour, which is also probably shaped by broader social and ecological variables that could not be measured in this study [11,17]. For example, in

common ravens (*Corvus corax*), exploratory behaviour was strongly modulated by social context [68]. Individuals classified as ‘fast’ explorers, based on their latency to approach a novel object when tested alone, approached novel objects more slowly when conspecifics were present, whereas ‘slow’ explorers did so more quickly. A similar influence of social context was recently observed in juvenile herring gulls (*Larus argentatus*) responding to novel objects [69]. In addition, observational learning and social cues may, over time, moderate or override the individual differences that are established early in life [70–73]. Young individuals often follow conspecifics to locate food [74–76], suggesting that social learning may facilitate the development of effective foraging strategies. Habitat characteristics can also shape spatial use independently of inherent behavioural differences between individuals [77–79]. Consequently, the link between pre-fledging exploratory behaviour and post-fledging foraging outcomes may shift over time in response not only to developmental processes but also to environmental conditions [80–82].

(c) Early exploratory phenotype and post-fledging behaviour do not predict survival

We found that more than half of the juveniles died within the first 6 months, highlighting once again the critical nature of the post-fledging period, when our study species face the additional challenges of migration [83]. Contrary to expectations, neither the exploratory phenotype nor post-fledging movement metrics were significantly associated with survival over the 6-month tracking period. One possible explanation is that the benefits and costs of exploration may have balanced each other out at the population level [11,84,85]. Alternatively, mortality may have been driven by environmental factors or stochastic events, such that the advantages or disadvantages of exploration alone were insufficient to affect overall survival during this complex phase. Finally, the relationship between exploration and survival could have been influenced by unmeasured individual characteristics, such as health or condition [86]. Taken together, these findings suggest that while exploratory behaviour may confer certain advantages, its influence on survival during the high-risk post-fledging period is probably context-dependent and shaped by multiple, interacting factors.

5. Conclusion

By linking pre-fledging exploratory behaviour with post-fledging movement and survival, our study shows that early-life behavioural variation can shape how juveniles interact with their environments. Identifying the sources of this variation is an important step towards understanding how behavioural diversity may influence population resilience to environmental change. Although pre-fledging exploratory phenotype predicted habitat preference, it did not explain variation in spatial use or survival, suggesting that some behavioural components remain closely linked to early life phenotypes, whereas others are more strongly shaped by post-fledging experience and environmental context. Nevertheless, our findings underscore the value of studying behavioural development within a life-history framework and of integrating experimental, ecological and high-resolution tracking approaches.

Ethics. All procedures performed in this study have been approved by the ethical committee of the University of Antwerp (file number CDE2021-03). The ethical committee has approved the use of 160 juveniles captured in the wild for the purpose of the research.

Data accessibility. The data are available via Zenodo [87] and Movebank, under study name [LBBG_JUVENILE](#). Intermediate data and scripts are provided through OSF [88].

Supplementary material is available online [89].

Declaration of AI use. We used AI-assisted technologies at the final stage of writing to assist with grammar and syntax correction.

Authors' contributions. M.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, software, validation, visualization, writing—original draft, writing—review and editing; L.M.: conceptualization, methodology, software, supervision, validation, writing—review and editing; E.S.: conceptualization, data curation, investigation, methodology, resources, validation, writing—review and editing; F.V.: conceptualization, funding acquisition, investigation, methodology, resources, validation, writing—review and editing; L.L.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing—review and editing; W.M.: conceptualization, funding acquisition, investigation, methodology, resources, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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