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LETTER

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Natal legacies cause social and spatial marginalization during dispersal

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Abstract
Early-life experiences can drive subsequent variation in social behaviours, but how differences among individuals emerge remains unknown. We combined experimental manipulations with GPS-tracking to investigate the pathways through which developmental conditions affect social network position during the early dispersal of wild red kites (*Milvus milvus*). Across 211 juveniles from 140 broods, last-hatched chicks—the least competitive—had the fewest number of peer encounters after fledging. However, when food supplemented, they had more encounters than all others. Using 4425 bird-days of GPS data, we revealed that this was driven by differential responses to competition, with less competitive individuals naturally spreading out into marginal areas, and clustering in central foraging areas when food supplemented. Our results suggest that early-life adversities can cause significant natal legacies on individual behaviour beyond independence, with potentially far-reaching consequences on the social and spatial structure of animal populations.

KEYWORDS
carry-over effects, development, early-life effects, individual phenotype, natal dispersal, prospecting, raptor, social network, sociality, transience

INTRODUCTION

Early-life experiences can significantly impact animal social behaviours, with far-reaching consequences for individuals and the emergent population structure (Belsky et al., 1991; Stanton & Mann, 2012). Despite the growing body of literature investigating how development shapes social outcomes (Brandl et al., 2019; Ilany et al., 2021; Kohn et al., 2022; Spencer, 2017), the behavioural mechanisms through which these patterns arise remain unclear. Developmental conditions could, for example, influence movement decisions (Meylan et al., 2002; Pakkala et al., 2016) and the social decisions that individuals make later in life (Farine et al., 2015). How such spatial (individual movement and space use) and social phenotypes (rules governing movement across varying social environments) together shape the social environment experienced by individuals is becoming a major theme in ecology (Webber et al., 2023). In this framework, natal factors may influence the establishment of different social and spatial phenotypes which interact with the environment to shape behavioural patterns and in return influence the environment animals experience (Cantor et al., 2021).

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While several intrinsic characteristics have been linked to differences in spatial and social phenotypes (Alves et al., 2013; Pusey, 1987; Turner et al., 2018), phenotypes are also plastic and may reflect the past or present conditions experienced. Developmental stress is often linked to both the social environment (i.e. sibling competition) and the availability of resources during growth (Kitaysky, 2001; Kitaysky et al., 2005; Will et al., 2014) which can affect, either independently or together, the physical (Mitchell et al., 2011; Saino et al., 2018) and cognitive (Kosten et al., 2006) characteristics at later life stages, contributing to traits associated with sociality (Aplin et al., 2013; Carere et al., 2005; Gartland et al., 2022). For instance, juvenile zebra finches undergoing experimentally increased developmental stress formed larger foraging groups and associated more randomly later in life than did controls (Boogert et al., 2014; Brandl et al., 2019). Yet, it remains unclear whether these patterns capture individual social choices or reflect other traits such as differential space use (Spiegel et al., 2016).

Juveniles that experience adverse conditions often reach independence in a physically weakened state (e.g. Nägeli et al., 2022; Perrig et al., 2017), affecting future competitive abilities (Spencer, 2017). For example, weaker individuals may seek fewer social encounters (Spiegel et al., 2017) by deciding against moving to (Cozzi et al., 2018) or settling in (Maag et al., 2018) resource-rich areas with high intraspecific competition (Royle et al., 2005). Weaker individuals who experienced adverse early-life conditions could also actively seek more social interactions, for example, if they value the social information of conspecifics higher than that of their parents (Farine et al., 2015). Thus, decisions in response to the social environment can affect space use. Alternatively, weaker individuals could simply move less, and in doing so encounter fewer conspecifics. Differentiating between mechanisms underlying social outcomes poses unique challenges as it requires to track where many individuals move and who they encounter (He et al., 2023). One solution is GPS tracking, which can simultaneously capture how individuals move relative to one another (Strandburg-Peshkin et al., 2015). When deployed at a large scale, GPS tracking can reveal previously hidden drivers and consequences of social structure within and between populations (e.g. Papageorgiou et al., 2019).

Here, we investigate the impact of early-life experiences on social and spatial phenotypes in wild juvenile red kites (*Milvus milvus*) by combining a food supplementation experiment during the nestling phase with GPS tracking during the early dispersal phase—the first independent phase preceding migration. Food supplementation has multiple effects on red kite nestlings, including improved body conditions (Nägeli et al., 2022), reduced stress levels (Catitti et al., 2022) in last-hatched individuals, and advanced the start of natal dispersal (Scherler, Witczak, et al., 2023). We test whether differences in food availability experienced by nestlings of different hatching ranks lead to distinct natal legacies (i.e. lasting effects arising from different developmental conditions) with respect to their sociality, movement patterns and space use. Using a stepwise approach, we partition natal effects on the tendency to leave the study population from the natal effects on the social and spatial phenotypes within it, characterized through social networks and analysis of individual movement and space use. Given the marked male-biased philopatry in the species (Evans et al., 2010; Literák et al., 2022), we expect high-quality (early-hatched, food supplemented) males to spend more time prospecting in the natal area, where important environmental and social cues can be collected to inform future dispersal strategies (Patchett et al., 2022). Further, we hypothesize that suboptimal developmental conditions affect juveniles' competitiveness (Mainwaring et al., 2023) and learning strategies (Farine et al., 2015; Fisher et al., 2006) such that low-quality (last-hatched, non-supplemented) individuals would rely more on social cues. Depending on the social environment (e.g. local conspecific density), we expect that the emerging motivation of low-quality individuals (i.e. social phenotype) will steer their spatial phenotype (e.g. increased movement activity, differential space use) to increase the number and the diversity of conspecific encounters (Figure 1).

METHODS

The study system and study area

Red kites are tree-nesting, opportunistic scavengers feeding mostly on small vertebrates but also on a variety of anthropogenic food (Andereggen, 2020; Cereghetti

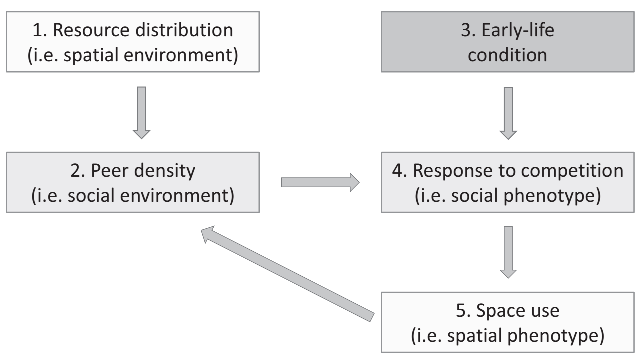

FIGURE 1 Conceptual diagram how early-life conditions influence the emerging spatial-social properties of red kites during the early dispersal phase. Resource distribution (box 1) influences how individuals distribute within the landscape (box 2). Favourable developmental conditions (box 3) increase the competitiveness of last-hatched red kites, thereby increasing their affinity for high-density social environments (box 4). Competitive last-hatched individuals gather in high-density foraging areas (box 5), hereby increasing social encounters, and further affecting the composition of the social landscape of the population (box 2). Shades of grey indicate the spatial dimension (light), social dimension (medium), and early-life condition (dark).

et al., 2019). The period from hatching to independence (i.e. departure from the natal home range) lasts approximately 90 days (Scherler, Witczak, et al., 2023). After independence, they start the first phase of dispersal, with some individuals remaining close to their natal home range and others performing large explorations (Aebischer & Scherler, 2021). Almost all swiss juveniles overwinter in central and southern France and Spain (Witczak et al., 2024) Our study population covers 387 km^2 in Western Switzerland, an area dominated by agriculture and managed forests, from 482 to 1763 m a.s.l. The local breeding density of red kites is among the highest worldwide (Aebischer & Scherler, 2021) and is lowest at high elevations and in central areas in proximity to cliffs (Figure S1).

Food supplementation treatment

During the breeding seasons from 2016 to 2018, we provided supplementary food to 78 broods by mounting a feeding platform (at 20–200 m distances) from each target nest. We placed 10 one-day-old dead chickens on each platform every second day during incubation and confirmed the parents' use of the platforms through field observations. After hatching, we added five chickens per nestling at each feeding round, and after the oldest nestling reached 10 days of age, we added 10 chickens per nestling and round (see Catitti et al., 2022 for details).

Measurement of nestling parameters and GPS tracking

We climbed each nest multiple times, starting when the nestlings were 15–20 days old (see Figure S2 for an overview of the field methods). During the first visit, we measured and ringed all nestlings for individual identification. We estimated nestling age based on wing length measurements, following a growth curve model given by Aebischer and Scherler (2021) and corrected for the effect of supplementary food on nestling growth (Nägeli et al., 2022), and assigned an age-based hatching rank to each nestling. Fledglings were sexed genetically using a small (~50 μL) blood sample from the brachial vein (see Nägeli et al., 2022 for details on sex determination). We tagged all juveniles between 38 and 42 days of age with solar powered GSM-GPS-UHF transmitters (N=255 Ecotone SKUA/CREX type, N=25 Milsar M9 type) with a backpack-style diagonal-loop harness (see Scherler, Witczak, et al., 2023 for further details).

Assessing the early dispersal phase

We defined the start of the early dispersal phase as the date of departure from the natal home range, defined as a 2 km radius around the nest, using net displacement curves following Scherler, Witczak, et al. (2023). The early dispersal phase ended with the start of fall migration. We excluded from the analysis all juveniles that either died before the start of dispersal or whose GPS data prevented us from clearly defining the phase duration (N=46, see Supporting Information). We focused on daytime activity by selecting only GPS fixes between 8 AM and 7 PM CET and homogenized the dataset by sub-setting the data to hourly fixes. We removed two individuals from analyses due to missing sex identification. In total, we described the early dispersal behaviour of 232 juveniles across 147 broods, of which 80 birds received supplementary food in the nest (N_{2016}=27 individuals from 20 broods, N_{2017}=45 individuals from 27 broods, N_{2018}=8 individuals from 5 broods), and 152 did not (N_{2016}=63 individuals from 43 broods, N_{2017}=63 individuals from 38 broods, N_{2018}=26 individuals from 14 broods).

Analyses

We performed all analyses in R version 4.2.1 (R Core Team, 2023). Analyses of social and spatial phenotypes were done in a Bayesian framework. Effects and corresponding parameter uncertainty are expressed as the median and 95% credible intervals (95% CrI) of the posterior distribution. We used a full model approach based on a priori hypotheses and only removed interactions when the 95% CrI overlapped 0 (Korner-Nievergelt et al., 2015).

Early dispersal types

Exploratory analysis of the movement trajectories during early dispersal revealed two distinct behavioural groups. One group exhibited a strong fidelity to their area of origin or nearby locations, while the other group left for large explorations without returning. A bimodal distribution of the proportion of the time spent in the study area (calculated as the proportion of hourly GPS fixes falling within the study area; see Figure S3) reflected this pattern, with proportions clustering near 0 or 1. Using this proportion as a proxy for the overall stationarity or exploratory behaviour, we fitted a fractional logistic regression using a generalized mixed-effect model with the package 'stats'. The model included feeding treatment in the nest (0/1) and hatching rank. We categorized hatching rank as being the last-hatched or not (early-hatched), because in red kites the largest size difference occurs between the last-hatched and the rest of the siblings, regardless of brood size (Scherler, van Bergen, et al., 2023). Singletons (N=74) were considered early-hatched. We included sex to check for intrinsic differences in early dispersal behaviour. To investigate whether supplementary feeding compensates for the potential rank disadvantage, we tested the interaction between feeding treatment and hatching rank. Finally, to account for the higher probability of individuals close to the border of the study area moving outside of it, we incorporated the distance of each individual first GPS location to the centroid of the study area as a covariate.

Social phenotype

We used GPS data to build daily, proximity-based social networks and describe social phenotypes. We selected only fixes within the study area, and removed all days when fewer than three tagged birds were present, totalling 211 juveniles, of which 75 were food supplemented (N_{2016}=25 from 19 broods, N_{2017}=43 from 27 broods, N_{2018}=7 from 4 broods) and 136 assigned to the non-supplemented control group (N_{2016}=51 from 38 broods, N_{2017}=60 from 38 broods, N_{2018}=25 from 14 broods). In our social networks, we deemed that two individuals were likely to have had social contact when the distance between them was less than 250 m, a distance at which red kite not only are aware of each other but can exchange social information (see Supporting Information). At every hourly interval, co-occurrence of dyads (two birds) of juveniles within 5-min sampling windows were marked as encounters using the package 'spatsoc' (Robitaille et al., 2019). The strength of association of each dyad (edge) was weighted by the number of times that the two birds had the opportunity to meet through an adaptation of the very simple ratio Index (Hoppitt & Farine, 2018):

$$\mathrm{SRI} = \frac{x}{x + y_{ab}},$$

where x represents the number of co-occurrences of each dyad and y_{ab} is the number of simultaneous detections of each bird in which their distance was greater than the threshold (see He et al., 2023 for details). This produced a matrix of weighted association strengths, from which we calculated individual (i) weighted degree (sum of individual weighted edges with all other possible individuals; a proxy for animal sociality) and (ii) differentiation of encounters using the coefficient of variation (CV) of individuals' edge weights. A low CV (low diversification) corresponds to all edges showing similar strength, while a high CV (high diversification) indicates a mixture of strong and weak edges. CV could only be calculated when individuals had two or more non-zero edges. While the single measure of these parameters represents the social environment experienced by each individual per day, we consider the tendency to repeatedly be near conspecifics—or not—and whether these repeated encounters are more or less differentiated, as the measure of social phenotype.

We modelled weighted degrees as a function of the natal factors using a Bayesian multilevel Hurdle-gamma regression (package 'brms', Bürkner, 2017). We used the same set of fixed effects (feeding treatment, hatching rank and sex) and interaction (feeding treatment × hatching rank) as the full early dispersal types model, but as social networks were built daily, we also included calendar date and individual as random intercepts to account for non-independence of data in time and across individuals. We further accounted for differences in the probability to encounter other GPS-tagged conspecifics due to the proximity to the periphery of the study area (i.e. where the density of GPS-tagged birds was lower). To do so, we calculated a daily 90% minimum convex polygon (MCP) of the whole population, using the package 'adehabitatHR' (Calenge, 2006), and added a binary covariate in the model with a '1' indicating individuals with all their fixes inside this MCP and a '0' for those with at least one fix outside. The encounter diversification was modelled analogously as the weighted degrees, using a Hurdle-gamma distribution for the response, where both parts (0 vs non-0, and only non-0s) were modelled with the same covariates. Additionally, we estimated weighted degrees and tested its relationship to natal factors at different spatial and temporal thresholds to assess if our methodological decisions affected the results.

Spatial phenotype

We investigated if individual differences in sociality were mirrored by distinct movement patterns (e.g. activity levels; *pattern-based spatial phenotype*, Webber et al., 2023) or varying space use (e.g. occurring in spatially structured or unstructured areas of different peer density; *process-based spatial phenotype*). We explored pattern-based spatial phenotypes to understand whether social encounters differences associated with varying extent of the area covered or activity levels beyond it. With the process-based space use, we further investigated whether social outcomes associated with individuals occurring in areas of different density (the social environment), and whether such areas were spatially defined.

To describe movement patterns, we calculated daily range size and average distance travelled for each individual included in the social network analysis, excluding bird-days with fewer than 5 GPS-fixes. We calculated the range size as the 95% of the utilization distribution (UD) using the package 'adehabitatHR'. The smoothing parameter (h) in the range estimation was set to the reference level for all individuals, as we only needed to compare the ranges among individuals and not make population-level inferences about habitat use. Average daily distance travelled was calculated using the 'adehabitatLT' package (Calenge, 2006). We assessed whether temporal autocorrelation in the data influenced our estimates by comparing range size and average step length estimates from 10 randomly selected individuals with those obtained from continuous-time movement models using the ctmm package (Calabrese et al., 2016), but as these analyses yielded high correlation (Pearson's $r > 0.8$, $p < 0.01$, Figure S4), we retained our original methods.

To describe process-based space use, we quantified peer density experienced by birds from different natal groups by measuring pairwise range overlap of their UDs (Bhattacharyya's affinity (BA) index, reviewed in Fieberg & Kochanny, 2005). If one group uses an area more intensively, we expect individuals from this group to have higher average UD overlap with all others. Second, we investigated whether differences in peer density were linked to specific geographical areas. For this, we assessed the spatial overlap between the 50% UD of the different natal groups (supplemented last-hatched, non-supplemented last-hatched, supplemented early-hatched, non-supplemented early-hatched) with the central foraging area ('CFA'), defined as the 20% UD of all GPS locations between 9 AM and 2 PM, the period of high foraging activity, using the BA index. A 50% UD overlap is a widespread methodology to examine core space use in animals (Orgeret et al., 2021; Rossiter et al., 2002). To conduct a significance test, we simulated 1000 overlaps by randomly exchanging group identity of individuals in each permutation (Farine, 2017) and scored the proportion of the simulated overlaps that were less than or exceeded the observed overlap, where the former indicates aggregation and the latter segregation. This measure of spatial segregation was calculated for all individuals across all years due to differences in yearly sample sizes, and under the assumption that the main environmental features driving movement decisions are stable across this time period. To verify if proximity to the nest of origin influenced the observed spatial patterns, we conducted a permutation test on nest identities.

We modelled daily range size and overlap and averaged daily distance travelled with multilevel Bayesian regression models with the 'brms' package, with either Gamma distribution (for daily distance and range size) or zero-inflated Beta distribution (pairwise range overlap). For the range size and daily distance models, we included the same covariate structure as the previous models and included individual ID and calendar date as random effects. In the range model, we additionally included the number of fixes (range = 5–12) used to calculate the daily range to correct for the positive trend observed between number of locations and range size (Figure S5). To assess natal effects on activity beyond the area covered, we added range size as covariate to the distance travelled model. The pairwise overlap was modelled as a function of the identity of the first individual of the pair (non-supplemented early-hatched, non-supplemented last-hatched, food supplemented early-hatched, and food supplemented last-hatched), and both IDs of the pair and the calendar date were added as random effects. Because we did not have prior knowledge on parameter distributions, we used default or weakly informative priors in all models (see Table S1 for a list of priors), and we checked the goodness of all model fits with graphical posterior predictive checking with the 'rstanarm' package (Gabry & Goodrich, 2023). We compared daily ranges and daily pairwise overlaps to weekly ones to ensure that the choice of our timescale did not bias the results.

RESULTS

We collected 109,710 hourly GPS fixes, resulting in 10,768 bird-days from 232 juveniles followed during their early dispersal phase. While hatching rank and treatment did not affect early dispersal types (Table 1), juveniles from different feeding treatment and hatching rank differed in their social and spatial phenotypes (Table 2).

Early dispersal types

The early dispersal phase lasted on average 46.2 days, showing substantial inter-individual variation (SD = 28.7, range = 1–140). Males prospected 11 days longer than females (median and 95% CrI: 10.9 days [3.5; 17.8]) and food supplemented individual prospected 8 days less than non-supplemented control birds (−7.9 days [−15.6; −0.1]). After accounting for their initial spatial location, juveniles of different hatching rank or feeding treatment did not differ in the proportion of time spent in the study area, but sex had an effect, with males spending on average more time (0.50 [0.42; 0.58]) than females (0.39 [0.33; 0.46]) (Table 1).

Social phenotype

We built 293 daily social networks that included a total of 211 individuals, recording a total of 9773 social encounters (mean number of encounters per network: 33.4, SD = 43.2). Each individual was present in an average of 24 networks (SD = 21.2, range = 1–90), yielding a total of 5063 measurements for the weighted degrees

TABLE 1 Parameter estimates and 95% Credible Intervals (95% CrI) from a fractional logistic regression of early-life conditions (feeding treatment and hatching rank) and sex on the proportion of time spent in the study area during early dispersal, controlling for the initial distance to the margin of the study area. Parameters whose 95 % CrI did not include 0 are reported in bold.

Parameter	Estimate	2.5%	97.5%
Food suppl. (1)	−0.03	−0.11	0.05
Last hatched (1)	0.01	−0.07	0.09
Sex (m)	**0.11**	**0.03**	**0.19**
Distance to edge (m)	**−0.21**	**−0.28**	**−0.15**

Note: Estimates are to be interpreted such that, for example, males are on average associated with a 11% percentage increase in the proportion of time spent inside the study area compared to females.

TABLE 2 Summary of the biological processes investigated, and statistical tests performed, including the results, interpretation and reference to tables and figures in the main text and Supporting Information.

		Response variable	Predictor			Interpretation	Tables and figures
Social process	Strength of sociality of individual	Weighted degrees	Feeding treatment × Hatching Rank		Sex	Food supplemented last-hatched juveniles have increased encounters	Table S2; Figure 2
	Differentiation of social encounters	CV (edge weights)	Feeding treatment	Hatching Rank	Sex	No effect	Table S3
Spatial process	Extent of the occupied area	Daily range size	Feeding treatment	Hatching Rank	Sex	Last-hatched have a smaller daily range	Table S5
	Activity	Daily distance travelled	Feeding treatment	Hatching Rank	Sex	No additional effect after controlling for daily range size	Table S5
	Density in the occupied area	Pairwise daily ranges overlap	Feeding treatment × Hatching Rank		Sex	Food supplemented last-hatched have a larger overlap of their daily range with that of other peers	Table S7; Figure S11
	Location of the occupied area	Spatial segregation with the CFA	Feeding treatment × Hatching Rank		Sex	Food supplemented last-hatched have the highest overlap with the CFA	Table 3; Figure 3

Note: Effects with a 95% CrI excluding zero are highlighted. The interactive effect between feeding treatment and hatching rank was always tested but kept in the final model only if the 95% CrI did not overlap zero.

(encounters of individuals) and 2285 measurements of encounters differentiation (CV of edge weights). On average, birds had 4.38 social encounters per day (SD = 2.68, range = 1–32, Figure S6A), but this was time-dependent due to the varying number of birds present in the study area (Figure S6A). Encounters occurred at an average distance of 109.6 m (SD = 68 m, range = 1.22–249.93 m; Figure S6B). While early-hatched individuals had comparable weighted degrees regardless of the feeding treatment, the strength of association of last-hatched was slightly weaker compared to their older siblings when non-supplemented, but it substantially increased when supplemented (Table S2; Figure 2). Encounter diversification was not affected by any of the natal factors (Table S3). The comparison at different spatial and temporal scales yielded compelling support for our estimates, both in terms of the weighted degrees measured (150–250 m threshold: Pearson's $r > 0.9$; 1–7 days network: Pearson's $r > 0.9$, Figure S7) and of the model estimates (Tables S2 and S4; Figures S8 and S9).

Spatial phenotype

We described daily movement behaviour and space use of 200 of the 211 juveniles used for the social phenotype analysis, for a total of 4425 bird-days. Last-hatched individuals had a smaller daily range than early-hatched, and male daily range tended to be larger than females (Table S5). Daily range sizes and distance travelled were strongly correlated (Pearson's $r = 0.73$, $p < 0.01$), with no additional natal effects on daily distance travelled (Table S5). The comparison between daily and weekly range estimates yielded similar trends, although the strength of the sex effects was stronger than that of hatching rank (Table S6; Figure S10). The differences in social phenotypes paralleled differences in the juvenile movement behaviour, with the range overlap of last-hatched birds considerably increasing if supplementary fed (Table S7), suggesting that the feeding treatment increased spatial clustering of last-hatched individuals. Males and females did not differ in their range overlap, and the same trend was observed when using weekly estimated ranges (Figure S11). The spatial segregation analysis suggests that this increased range overlap was due to a preference—showed by all juveniles, but especially by food supplemented last-hatched—towards the CFA (overlap = 0.40, p-value = 0.08; Table 3; Figure 3). Indeed, despite being all attracted to the most central area, members of the other natal groups extended their core range, with food-supplemented early-hatched stretching towards eastern regions while non-supplemented last-hatched rather occurring in south-western ones (Figure 3b). These patterns of space use according to natal hatching rank and food supplementation were not driven by nest site distribution (Table 3). The yearly patterns showed that despite the

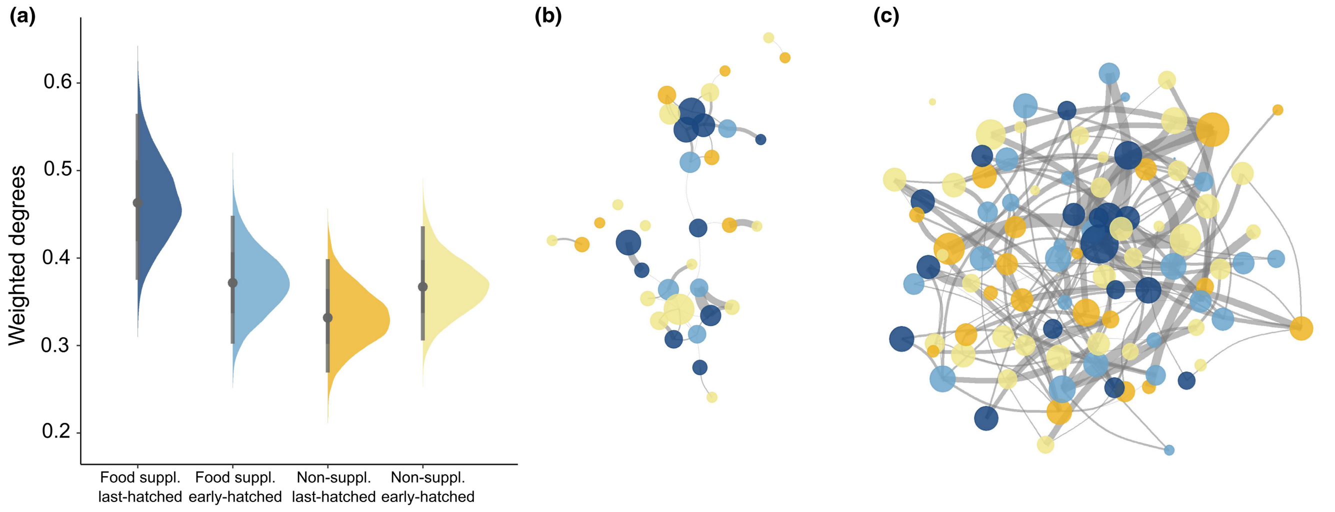

FIGURE 2 Food supplementation during growth influenced the subsequent social position of juvenile red kites. (a) Median (dots) and 95% credible intervals (95% CrI) of the posterior predictive distributions (bars) for the interactive effect of hatching rank and supplementary feeding on red kite juveniles' weighted degrees, a measure of intensity of social encounters. (b, c) Example of social networks measured in a day, and over the whole season, respectively. The size of the node is proportional to the corresponding weighted degrees, and the width of the edge is proportional to the weighted edge of each dyad. In (c), only the two strongest edges per node were retained for graphical purposes.

TABLE 3 Spatial segregation or aggregation of birds of different natal groups with the central foraging area (CFA).

ID group	Observed	Simulated mean ± SD	Interpretation	*p*-value	Number of nests included	Simulated mean ± SD	*p*-value
Non-suppl. early-hatched	0.28	0.30 ± 0.3	Segregation	0.25	12	14.30 ± 2.56	0.13
Non-suppl. last-hatched	0.29	0.31 ± 0.05	Segregation	0.41	9	10.30 ± 2.57	0.25
Food suppl. early-hatched	0.33	0.30 ± 0.05	Aggregation	0.24	11	10.30 ± 2.42	0.32
Food suppl. last-hatched	0.40	0.30 ± 0.07	Aggregation	0.08	4	6.44 ± 2.08	0.07

Note: Shown are observed vs. simulated overlaps of the daily 50% utilization distributions (UDs) with the CFA (Bhattacharyya Affinity Index). If the observed overlap was larger or smaller than that extrapolated from 1000 simulation, we interpret it as aggregation or segregation, respectively. The number of nests included in the UD of each natal group was also compared to that from simulations to test whether the extent of the UDs were influenced by the nest locations.

high overlap with the CFAs was not always a prerogative of the food supplemented last-hatched, they were consistent in the centrality of their location (Figure S12; Table S8).

DISCUSSION

Despite the undeniable evidence linking social behaviour to fitness (Ellis et al., 2019; Silk et al., 2009; Snyder-Mackler et al., 2020), the mechanisms underlying the emergence of social outcomes, and therefore their fitness effects, largely remain unclear. Developmental conditions have been previously suggested to shape the future social trajectories of individuals (Boogert et al., 2014; Brandl et al., 2019) and adversely affect individual fitness (Sergio et al., 2022). Our study substantially extends this work by experimentally demonstrating that developmental conditions influence later-life sociality and individual space use. This finding underscores the significance of natal legacies in shaping the social environment that individuals experience throughout their lives.

Under natural conditions, last-hatched individuals encountered fewer peers compared to earlier hatched individuals. However, the provision of supplementary food resulted in a significant increase in encounters for the last-hatched group. This increase was paralleled by a spatial process: last-hatched individuals switched from occurring in spread-out areas when not supplemented to clustering in the central areas, independently of the location of their nest of origin, when supplemented. This was not mirrored by an increase in overall activity, as the daily range size and distance travelled of last-hatched was reduced compared to early-hatched, irrespective of the feeding treatment. These findings suggest that developmental conditions can influence the motivation of juvenile birds to move in dense social environments during the early dispersal phase, and thus that the social phenotype (their response to competition) influences a process-based spatial phenotype (differences in space use) (as proposed in Figure 1).

Early-life conditions did not influence the overall early dispersal types (i.e. the proportion of time spent in the study area during the early dispersal phase),

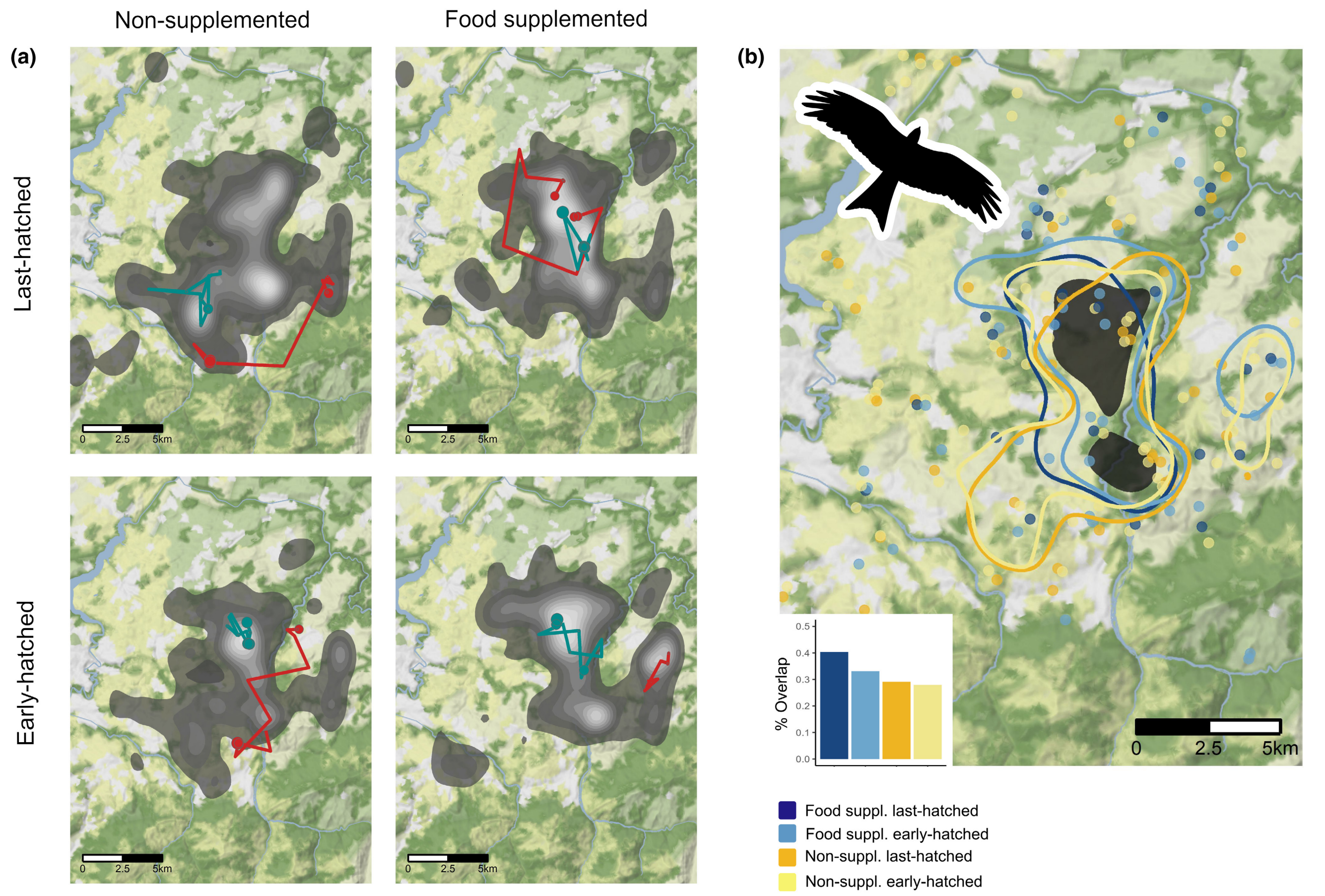

FIGURE 3 The effects of food provisioning on social position are manifested in differential space use by juveniles that were food supplemented and non-supplemented as nestlings. (a) Examples of daily movement paths for two individuals (red and blue) for each combination of natal category (top left: Non-suppl. last-hatched, top-right: Food suppl. Last-hatched, bottom-left: Non-suppl. early-hatched, bottom-right: Food suppl. early-hatched). Points indicate the locations in which the social encounters occurred. The point size is proportional to the number of encounters occurred in the given location. In the background are the density polygons (KDE) of the GPS locations of each natal group. (b) Lines are the polygon contours of the 50% utilization distribution (UD) of each natal group. Black polygon indicates the central foraging area (CFA), calculated as the 20% UD of all GPS locations. Points indicate nest locations of each natal group. At the bottom-left, percentage of overlap between the group UDs and the CFA (maximum overlap=0.5).

indicating that the decision to stay or leave altogether were not dependent on the individual's condition. However, it is important to note that our results do not exclude the existence of a relationship between physical or physiological condition and early dispersal strategies, as demonstrated by previous studies (Kingma et al., 2016; Mares et al., 2014), because red kites can perform long-distance explorations in a matter of days or weeks (Aebischer & Scherler, 2021), and detecting these was not a focus of our approach. Further, natal dispersal in red kites continues for several years after returning from the first migration (Orgeret et al., 2023), so early-life effects on dispersal strategies may become visible only at later phases of natal dispersal. Males spent proportionally more time in the study area than females, consistent with the general dispersal pattern in birds (Greenwood & Harvey, 1982) whereby females tend to disperse further than males. Our results suggest that sex-specific differences in dispersal behaviour can start during the very early phase of natal dispersal, indicating an inherent stronger propensity for long-distance natal dispersal in females starting just after independence (Reed et al., 1999).

Food-supplemented last-hatched individuals clustered in areas with low breeding density (Figure S1), unlike non-supplemented last-hatched individuals. While clustering with other individuals can bring benefits by decreasing foraging costs through communal searching effort and providing access to information about potential future breeding sites (Dwyer et al., 2018; Pärt et al., 2011), it also introduces burdens such as competition and disease transmission, that non-supplemented last-hatched individuals are less able to support (Ranta et al., 1993). As in other birds of prey species, last-hatched red kite nestlings typically reach fledging age in the worst physical and physiological conditions of all siblings (López-Jiménez et al., 2016; Müller et al., 2011; Nägeli et al., 2022) and develop poorer social skills in the nest (Catitti et al., 2023; Magrath, 1990), which can hinder access to environments that provide information about foraging opportunities (Farine et al., 2015; Mesoudi et al., 2016). However, when food supplemented in the nest, last-hatched juveniles strongly improved both their physical and physiological status at fledging (Catitti et al., 2022) possibly affecting their competitive potential at later stages and allowing them to access central, higher competition areas. This suggests that favourable food conditions in the nest results not only in the reduction of within-brood differences in fledging condition but also in later behavioural decisions.

Raptors like red kites are known to forage in groups over agricultural fields and anthropogenic sources such as dumpsters and private feeders (Aebischer & Scherler, 2021). Anthropogenic feeding sites are most prevalent in the easternmost regions of the study area, primarily visited by early-hatched juveniles (see Cereghetti et al., 2019 for a map of anthropogenic feeding sites). At these anthropogenic feeding hotspots, dozens of red kites compete for the clumped, rich food sources. Early-hatched juveniles are expected to have higher competitive abilities due to their enhanced physical condition and competitive experience in the nest (Dey et al., 2014; Drummond, 2006), making them more likely to exploit these anthropogenic food sources compared to their last-hatched peers. Indeed, non-supplemented last-hatched individuals extended their space use to south-western regions, characterized by lower breeding densities (Figure S1) and no known anthropogenic feeding sites (Cereghetti et al., 2019) suggesting that early-life conditions contribute shaping a condition-dependent habitat use.

While the combination of local enhancement tactics, attraction towards foraging conspecifics (Poysa, 1992) and resource distribution (Roshier et al., 2008) influences the motivation of individuals to forage in certain areas, the way animals navigate through this environment is associated to their phenotype (Cote et al., 2017; Cote & Clobert, 2006). We show that these phenotypes are at least partially driven by the social and resource conditions experienced in the nest. Favourable developmental conditions allowing individuals to seek high-density areas highlight how early life affects behavioural decisions in the face of spatial (resource distribution) and social (conspecific density) environments, shaping the population's social landscape (Figure 1). As the movement activity (daily range size and distance travelled) was unrelated to the feeding treatment, the increased social encounters of food-supplemented last-hatched individuals were not a result of heightened activity. Instead, differences in their response to the social environment (i.e. their social phenotype) influenced space use with consequences on the social outcomes, creating a feedback loop to the social environment. Importantly, by affecting social and spatial phenotypes, different developmental trajectories affect the quality of information collected during the early dispersal phase. These processes have the potential to alter future behaviour, bearing significant consequences for the spatio-temporal dynamics of territory settlement, reproductive success, and survival (Ciaglo et al., 2021; Cox & Kesler, 2012; Jungwirth et al., 2015; Patchett et al., 2022; Schuett et al., 2012).

Numerous studies emphasize the importance of considering both social and spatial factors when examining animal decision-making (Fokkema et al., 2021; Spiegel et al., 2017; Toscano et al., 2016; Webber et al., 2023). However, empirical research investigating the mechanisms that operate at the intersection of these two dimensions—and especially in terms of their relative importance in shaping the social environments of individuals—remains rare (but see Albery et al., 2021; Yang et al., 2021). Our study represents a crucial first step in addressing this gap from the perspective of the effects of early-life conditions on sociality and space use. A question that emerges from our study is whether differences in social and spatial phenotypes during early dispersal are reinforced or attenuated over time (Jones et al., 2020; Webber et al., 2020). If phenotypes persist, the spatial and social marginalization of juveniles growing in the most adverse conditions may, for instance, develop into long-distance dispersal events (Matthysen, 2005). This would allow to reconstruct the full mechanistic pathway through which early-life conditions shape consistent inter-individual behavioural differences which can have far-reaching implications for individual fitness and population structure.

AUTHOR CONTRIBUTIONS

B.C., U.G.K. and M.U.G. conceived the study idea. D.R.F. contributed to the general conceptual framework of the study. B.C. collected and analysed the data and wrote the first draft of the manuscript. All authors discussed the results and contributed to the final version of the manuscript.

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DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are publicly available at http://doi.org/10.5281/zenodo.10226837.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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