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Extra food provisioning does not affect behavioral lateralization in nestling lesser kestrels

Camilla SORAVIA[a]*, Angelo BISAZZA[bc], Jacopo G.CECERE[d], and Diego RUBOLINI [iD] [ef]

[a]Centre for Evolutionary Biology (M092), University of Western Australia, 35 Stirling Highway, Perth, WA 6009, Australia, [b]Department of General Psychology, University of Padova, via Venezia 8, Padova I-35131, Italy, [c]Padova Neuroscience Center, University of Padova, Via Orus 2/B, Padova I-35129, Italy, [d]ISPRA—The Italian Institute for Environmental Protection and Research, via Cà Fornacetta 9, Ozzano dell'Emilia, Bologna I-40064, Italy, [e]Dipartimento di Scienze e Politiche Ambientali, Università degli Studi di Milano, via Celoria 26, Milano, I-20133, Italy, and [f]Istituto di Ricerca Sulle Acque, IRSA-CNR, Via del Mulino 19, Brugherio I-20861, Italy

*Address correspondence to Camilla Soravia. E-mail: camilla.soravia@research.uwa.edu.au.

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Abstract

Costs and benefits of brain lateralization may depend on environmental conditions. Growing evidence indicates that the development of brain functional asymmetries is adaptively shaped by the environmental conditions experienced during early life. Food availability early in life could act as a proxy of the environmental conditions encountered during adulthood, but its potential modulatory effect on lateralization has received little attention. We increased food supply from egg laying to early nestling rearing in a wild population of lesser kestrels *Falco naumanni*, a sexually dimorphic raptor, and quantified the lateralization of preening behavior (head turning direction). As more lateralized individuals may perform better in highly competitive contexts, we expected that extra food provisioning, by reducing the level of intra-brood competition for food, would reduce the strength of lateralization. We found that extra food provisioning improved nestling growth, but it did not significantly affect the strength or direction of nestling lateralization. In addition, maternal body condition did not explain variation in nestling lateralization. Independently of extra food provisioning, the direction of lateralization differed between the sexes, with female nestlings turning more often toward their right. Our findings indicate that early food availability does not modulate behavioral lateralization in a motor task, suggesting limited phenotypic plasticity in this trait.

Key words: development, laterality, preening, raptor, sex-differences.

Lateralization is a common feature of vertebrate (Ocklenburg and Güntürkün 2012; Stancher et al. 2018) and invertebrate (Frasnelli et al. 2012; Niven and Frasnelli 2018) brains. It results from structural asymmetries and a division of cognitive functions between the left and right sides of the brain. This functional organization increases cognitive performance by allowing separate and parallel processes in the 2 halves of the brain (Güntürkün and Ocklenburg 2017; Rogers 2017, 2021). However, cerebral lateralization is not advantageous in all situations. Due to functional lateralization, different stimuli are preferentially processed by one side of the brain resulting in sensory and motor biases. For example, lateralized individuals may miss foraging or mating opportunities when stimuli are

located on the opposite hemisphere to where that specific sensory input is processed (Chiandetti 2011; Templeton et al. 2012). Lateralization can also hinder performance when the integration of sensorial inputs from the left and right side is required, such as during the navigation of cluttered environments and obstacle negotiation (Brown and Braithwaite 2005; Dadda et al. 2009).

Costs and benefits of a lateralized brain can vary with environmental conditions (Manns 2021). For example, in 2 teleost fish species, populations from high predation sites are more strongly lateralized than populations from low predation sites, likely because stronger lateralization improves multitasking, escape, and schooling performance (Brown et al. 2004; Hulthén et al. 2021). Mechanisms allowing for such adaptation have only recently begun to be understood (Güntürkün and Ocklenburg 2017; Manns 2021). Brain lateralization is a complex phenomenon, which depends on genetic, epigenetic, environmental factors, and their interactions (Ambeskovic et al. 2017; Schmitz et al. 2017; Wiper 2017). Growing evidence indicates that laterality is adjusted to local conditions through adaptive phenotypic plasticity: the environmental conditions experienced by the mother or by the individual itself during early life influence the development of cerebral lateralization to match the environmental conditions encountered later in life (Broder and Angeloni 2014; Ferrari et al. 2015; Chivers et al. 2016). Accordingly, recent laboratory experiments have shown that maternal or embryo exposure to visual or chemical cues signaling predator presence increases the strength of lateralization in cephalopods (Jozet-Alves and Hébert 2013), fish (Broder and Angeloni 2014; Ferrari et al. 2015; Dadda et al. 2020), and amphibians (Lucon-Xiccato et al. 2017). Even in the absence of direct predator cues, embryonic and larval development under low vegetation cover increased the lateralization of swimming behavior in *Pelophylax esculentus* tadpoles (Lucon-Xiccato et al. 2020).

Several other environmental factors are known to affect lateralization development. For example, light intensity and exposure duration during ontogeny determine the strength of lateralization in teleost fish, pigeons *Columba livia*, and domestic chicks *Gallus domesticus* (Rogers 1982; Dadda and Bisazza 2012; Chiandetti 2017; Letzner et al. 2017). It has been suggested that in the wild, high levels of intraspecific competition or predation risk could induce the hen to change the amount of time spent at the nest or to choose a particular nest site, and thus produce a progeny that can better cope with such environmental conditions (Vallortigara and Rogers 2005; Rogers 2010a).

Among the most common factors influencing laterality are prenatal and postnatal environmental stressors experienced by the mother or by the individual during early life. For example, maternal stress during pregnancy affects the degree and direction of offspring turning preference in brown rats *Rattus norvegicus* (Fride and Weinstock 1989; Alonso et al. 1991). Similarly, juvenile teleost and elasmobranch fish reared in stressful environmental conditions (increased water temperature and CO_2 concentration) show changes in the strength and direction of turning bias (Domenici et al. 2014; Sampaio et al. 2016; Maulvault et al. 2018; Vila Pouca et al. 2018). Such changes in behavioral lateralization in fish have also been linked to parasite infection (Roche et al. 2013) and exposure to pesticides (Besson et al. 2017).

So far, the majority of studies on the effect of environmental factors on the development of behavioral lateralization have been carried out in a laboratory setting (Güntürkün and Ocklenburg 2017; Ocklenburg et al. 2021). However, a focus on the lateralization of spontaneous behaviors in wild animal populations (e.g., Blumstein et al. 2018; Karenina et al. 2018; Romano et al. 2022) is needed to understand what ecological factors drive variation in the direction and strength of lateralization. Hence, there has recently been a call for studies manipulating environmental conditions in the wild to shed light on the plasticity of lateralization in response to ecological demands (Manns 2021).

Food shortage during breeding is considered a major stressor for parents and offspring (White 2008). While data on the influence of food availability on the development of laterality are scarce, there is considerable evidence that the strength of individual lateralization affects foraging efficiency. For example, behavioral lateralization has been associated with greater foraging efficiency in primates (McGrew and Marchant 1999), cetaceans (Friedlaender et al. 2017), birds (Güntürkün et al. 2000; Magat and Brown 2009; Karenina and Giljov 2022), and fish (Kurvers et al. 2017). Additionally, in fish and birds, lateralized individuals forage more efficiently than non-lateralized individuals under predation risk (Rogers et al. 2004; Dharmaretnam and Rogers 2005; Dadda and Bisazza 2006; Beauchamp 2013). Therefore, if food availability during early life acts as a signal of the environmental conditions encountered later in life, food scarcity should favor the development of more lateralized phenotypes. However, to our knowledge, this hypothesis has not been empirically tested. This effect of food availability on lateralization development could occur both prenatally, by varying the nutrients available to the embryo, or postnatally, by altering competition for resources during rearing.

In this study, we performed a food supplementation experiment and recorded nestlings' behavioral lateralization in a wild population of lesser kestrels *Falco naumanni*. The lesser kestrel is a diurnal raptor characterized by moderate sexual dimorphism, with adult females being on average 15% heavier than males (Podofillini et al. 2019). We simulated a natural condition of high prey availability by providing extra food to half of the experimental nests from egg laying to early nestling rearing (Podofillini et al. 2019; Soravia et al. 2021) and we subsequently quantified nestling behavioral lateralization from head turning during preening (Gaillard et al. 2017; d'Antonio-Bertagnolli and Anderson 2018).

Previous research has shown that environmental fluctuations in prey availability have a major impact on lesser kestrels' reproduction (Bonal and Aparicio 2008; Catry et al. 2012, 2017). Food scarcity increases nestling mortality due to starvation (Negro et al. 1993) and increases sibling competition for access to food resources, which takes the form of begging scrambles and repeated prey thefts (Soravia et al. 2021). In the study population, extra food provisioning from egg laying to early nestling rearing did not affect maternal body condition but enabled females to produce heavier eggs and improved nestling growth (10% higher body mass gain) (Podofillini et al. 2019). Given that lateralization enhances motor skills (e.g., Hunt et al. 2006; Grace and Craig 2008; Bell and Niven 2016) and performance in dual tasks (e.g., Rogers et al. 2004; Beauchamp 2013), stronger lateralization may be promoted under lower food availability (both prenatally and postnatally) and high intrabrood competition (postnatally). Therefore, we predicted that food-supplemented nestlings would display reduced lateralization compared with control nestlings because extra food provisioning decreases the advantage of lateralized phenotypes.

Additionally, we expected the effect of extra food provisioning on nestling lateralization to differ between male and female nestlings because females in this species reach a larger body size and thus likely have higher energetic demands during development (Anderson et al. 1993; Krijgsveld et al. 1998; Braziotis et al. 2017).

Accordingly, previous research has shown that the rate of aggressive interactions is higher in female-biased broods compared with male-biased broods, but this difference is no longer present after extra food provisioning (Soravia et al. 2021). Hence, we expected females to be more lateralized than males among control nests but not among food-supplemented ones.

Materials and Methods

General methods

Lesser kestrels are small (ca. 120 g) diurnal raptors that nest in pre-existing cavities in large breeding colonies and forage in the surrounding countryside, feeding mainly on invertebrates (Coleoptera, Orthoptera) and small vertebrates (lizards, rodents) (Rodríguez et al. 2010; Di Maggio et al. 2018; Cecere et al. 2020). It is estimated that south-eastern Italy hosts approximately 15% of the European population of lesser kestrels, of which ca. 1,000 pairs breed in the city of Matera (40°39′57″ N, 16°36′16″ E) (La Gioia et al. 2017; Morganti et al. 2021). Here, over a hundred nest-boxes were placed on the roof terraces of public buildings in the old town as part of conservation measures established to counteract the reduction in availability of nesting sites due to urbanization and refurbishment of old buildings (Iñigo and Barov 2010; La Gioia et al. 2017). These nest-boxes were rapidly occupied by lesser kestrels, facilitating the access to nests and monitoring of breeding attempts by researchers (Podofillini et al. 2018). The present study was performed on this wild population of lesser kestrels breeding in nest-boxes between April and July 2016. Nest-boxes were regularly inspected 3 times a week from the beginning of the breeding season. Lesser kestrels lay on average 4 eggs and incubation lasts approximately 30 days (Podofillini et al. 2019). Starting from the last 10 days of incubation, females were captured at the nest and their keel length, an indicator of body size, was measured using an analogical calliper (accuracy 0.1 mm) and body mass was measured using a digital top-pan scale (accuracy 0.1 g). We then calculated the scaled mass index (SMI, hereafter) as a measure of maternal body condition (see Podofillini et al. 2019). The SMI standardizes body mass at a fixed value of a linear body measurement (keel length in our case) based on the scaling relationship between mass and length (Peig and Green 2009, 2010).

At hatching, nestlings were individually marked with a non-toxic black permanent marker and weighed on a digital top-pan scale (accuracy of 0.1 g). Lesser kestrels' clutches hatch asynchronously, with an average of 2 days elapsing between hatching of the first and last egg, producing a hierarchy in size between siblings (Podofillini et al. 2018, 2019). Therefore, nestlings within the same brood were ranked according to hatching order from rank 1 (first-hatched) to a maximum of rank 5 (last-hatched) and when 2 nestlings were found hatched on the same visit at the nest, the one with the higher body mass was assigned the higher rank (Podofillini et al. 2019). At 8–10 days after hatching of the first egg, we weighed nestlings on a digital scale (accuracy 0.1 g) and collected a blood sample (ca. 200 μl) in capillary tubes by puncturing the brachial vein with sterile needles for molecular sexing (see Costanzo et al. 2020). Sexing was performed by PCR amplification of the CHD-1 gene located on the avian sexual chromosomes, following standard protocols (Griffiths et al. 1998; Costanzo et al. 2020). Nestling body mass was recorded again 15–16 days post-hatching of the first egg (hereafter "post-hatching" for brevity).

Food-supplementation experiment

The data were collected as part of a larger food supplementation experiment involving 100 nest-boxes (see Podofillini et al. 2019). A total of 26 nests (13 nests supplemented with food and 13 control nests) were randomly chosen for videorecordings to assess nestling behavioral lateralization. Food supplementation consisted of thawed laboratory mice Mus musculus (20 g per item) placed inside the nest-boxes. We used mice because small rodents represent a high percentage of the total biomass consumed by wild lesser kestrels during breeding (Di Maggio et al. 2018) and they were also easier to store and provide to nestlings compared with other typical prey (invertebrates, lizards). Food supplementation started when the nest-box was identified as occupied, that is, when the first egg was found in the nest, and stopped at the end of the early rearing stage (8–10 days post-hatching). The amount of extra food provided varied depending on the breeding phase: 3 mice every 2 days during egg laying and after hatching and 1 mouse every 2 days during the incubation period (see Podofillini et al. 2019). To standardize disturbance, control nests were inspected in the same way and with the same frequency as food-supplemented ones, simulating mice insertion into the nest-box (Podofillini et al. 2019). Food-supplemented nests were always checked for remainders on the following visit to confirm that the mice were eaten. During egg laying and incubation, the mice were likely eaten by the female, as during this time females are more often found inside the nest and receive feedings from the male (Donázar et al. 1992; Cramp 1998). After hatching, we confirmed that the parents were feeding the mice to the nestlings by installing a video camera after placing mice in the nest (Soravia et al. 2021).

Videorecording started once food supplementation finished. Each brood was filmed once between 8- and 22-days post-hatching, which covers the time window when preening behavior can be recorded inside the nest because nestlings are active from 8 to 10 days post-hatching and after 20–22 days they regularly exit the nest-box (Cramp 1998; Soravia et al. 2021). During each visit, we placed 2 digital cameras (Kodak playfull waterproof videocamera, 720p HD) in a control and food-supplemented nest, respectively. Before visiting the nests, each camera (size $5.58 \times 9.39 \times 1.27$ cm) was fixed to a wooden panel ($30 \times 30 \times 2$ cm) that was identical to the front wooden panel closing the nest-boxes (for details, see Podofillini et al. 2018); in this way, the camera could then be placed simply by unscrewing the original panel and replacing it with the panel bearing the camera. Individual markings on nestlings were used for identification on footage. The entire procedure of marking the chicks and replacing the front panel took less than 5 min for each nest. Additionally, nestlings were never recorded on video showing antipredatory responses toward the camera (e.g., freezing and avoidance), indicating that the presence of a camera caused minimal disturbance to nestlings. Cameras were powered by portable powerbanks (4,400 mAh) and they recorded until battery's exhaustion (up to 7 h). However, due to overheating (temperature loggers on rooftops reached 52°C), occasionally the battery failed, producing shorter videos. We examined only videos lasting at least 1 h because a pilot analysis showed that shorter videos entailed less than 10 preening observations per individual. As a consequence, our sample size was reduced to 13 food-supplemented nests (41 individuals) and 11 control nests (33 individuals). Each nestling was filmed on average 264 ± 118 SD min (range: 68–472 min) and the average duration of videorecordings did not differ between treatments (Mann–Whitney U-test: $Z = -1.32$, $P = 0.188$).

Assessment of laterality

Preening was identified as a movement of the nestling's head followed by feathers' displacement with the beak. The behavior was observed on average 45.7 ± 31.4 SD times per nestling (range: 3–138; $N = 74$ nestlings). We used the direction of the head's motion, that is, leftward or rightward, as a criterion to distinguish left and right preening, avoiding the ambiguity when the preened area was on the breast or the back and not on the sides of the body. Following previous studies on behavioral lateralization (Bisazza et al. 2000; Hoffman et al. 2006; Reddon and Hurd 2009; Gaillard et al. 2017), we computed a laterality index for preening: the difference between the total number of preening motions to the right (R) and the total number of preening motions to the left (L), divided by the total number of preening motions, that is, $(R - L)/(R + L)$. Positive values of the index indicate a bias to the right and negative values a bias to the left. The actual value of the index reflects the "direction" of lateralization, whereas the absolute value of the index gives a measure of the "strength" of lateralization.

Statistical analyses

General approach

We fitted linear mixed models (LMMs) with the direction or strength of lateralization as a response variable and brood identity as a random effect for all analyses. After confirming that preening frequency did not differ between experimental groups, we selected nestlings for which more than 9 preening bouts were observed ($N = 64$ nestlings, 26 from 9 control nests and 38 from 12 food-supplemented nests), allowing for a reliable estimate of behavioral lateralization according to previous studies (e.g., Reddon et al. 2009; Domenici et al. 2014; Karenina et al. 2016). Data from 1 control brood were omitted in all the models including sex because sexing was not possible for 1 control nest, leading to a final sample size of 61 nestlings (23 from 8 control nests and 38 from 12 food-supplemented nests). We checked this subsample for differences in maternal body size (keel length), nestling sex, brood size, brood sex ratio (proportion of males), and nestling age at the time of videorecording between the 2 experimental groups.

Before examining laterality, we checked if extra food provisioning improved nestling body mass in broods at 8–10 and 15–16 days post-hatching, respectively, using 2 LMMs with body mass as dependent variable and maximum brood size, food supplementation ($0 = $ control; $1 = $ food-supplemented), sex (female = 0, male = 1), and rank, as well as the 2-way interaction terms between food supplementation and brood size, sex, and rank as fixed effects.

Statistical analyses were performed using R version 4.1.2 (R Core Team 2021). Yeo–Johnson transformations were computed with the "bestNormalize" package (Peterson 2017) to normalize the distribution of the hourly frequency of preening and the strength of lateralization. LMMs were fitted using the "glmmTMB" package (Brooks et al. 2017). We checked the normality of residuals, homoscedasticity, and dispersion with the package "DHARMa" (Hartig 2021). In LMMs, all continuous predictors were mean-centered. Non-significant interaction terms were dropped from the initial model in a single step.

The effect of extra food provisioning on behavioral lateralization

First, we examined whether each nestling had a significant bias for rightward or leftward preening by binomial tests. Second, we evaluated the existence of a population-level lateralization for preening behavior by means of an intercept-only LMM with the direction of lateralization as a response variable both on 1) the entire sample of nestlings and 2) separately for males and females. Then we determined whether extra food provisioning affected the strength and the direction of lateralization by means of 2 LMMs. The fixed effects in these models were food supplementation, sex, rank, and brood size at the time of videorecording, as well as the 2-way interactions between food supplementation and sex, rank, and brood size. We did not include sex ratio in these models because it was highly correlated with nestling sex (Pearson's $r = 0.62$) and because models including sex ratio instead of sex were invariably less supported by the data (i.e., had higher AICc values; details not shown for brevity). We also did not include age in these models because it was negatively correlated with brood size at videorecording (Pearson's $r = -0.41$). However, the inclusion of age instead of brood size did not affect the results (see Supplementary Table S5). In the case of a lack of a significant effect of food supplementation on the strength or direction of lateralization, we then used the R package "BayesFactor" (Morey and Rouder 2021) to compute the Bayes Factor (BF, hereafter) comparing the LMMs including and excluding food supplementation as a predictor (all other main effects being retained in the respective models). The BF indicates whether it is more plausible to obtain the observed data under a model that includes or excludes an effect of food supplementation. This allowed us to disentangle between non-significance due to low statistical power or due to actual absence of an effect of food supplementation on lateralization (Harms and Lakens 2018).

Finally, due to unsuccessful capture of the female parent at 2 control nests, we were able to measure maternal body condition for 18 nests only ($N = 18$ nestlings from 6 control nests and $N = 38$ nestlings from 12 food-supplemented nests). Therefore, to test whether maternal condition influenced the strength or direction of lateralization, we fitted 2 additional LMMs with female SMI, nestling sex, nestling rank, and the 2-way interaction terms between female SMI and nestling sex and rank as fixed effects.

Results

Lesser kestrel nestlings preened on average 10.6 ± 7.8 *SD* times per hour (range: 1–39 times per hour, $N = 74$), and the frequency of preening behavior did not differ between experimental groups (estimate $\pm$ SE $= -0.03 \pm 0.36$, $Z = -0.08$, $P = 0.94$). The 2 experimental groups did not differ for maternal body size (keel length), nestling sex, brood size, brood sex ratio, and nestling age at the time of videorecording (Supplementary Table S1).

Overall, nestlings showed weak lateralization for preening behavior (median strength of lateralization $= 0.12$; range 0–0.38). Binomial tests detected only 8 individuals out of 61 (13%) with a significant turning preference; of these, 4 individuals showed a rightward bias and 4 a leftward bias (Supplementary Table S4). However, the lateralization in the studied population could be higher. Indeed, for a lateralized individual with a probability of turning on one side of 70%, at least 46 observations would have been necessary to have an 80% power of detecting it as significantly lateralized in a binomial test. Considering only individuals with 40 or more observations ($N = 41$), the proportion of lateralized individuals in our study population became 20%.

We found no significant preference for turning the head rightward or leftward at the population level (intercept estimate $\pm$ SE $= 0.01 \pm 0.02$, $Z = 0.43$, $P = 0.67$). However, when we considered female and male nestlings separately, we found that female nestlings had a significant rightward preference (intercept

Table 1. Effects of extra food provisioning on (a) the strength and (b) the direction of nestling lateralization

Predictors	Estimate (±SE)	Z	P
(a) Strength of lateralization			
Food supplementation	−0.21 (±0.27)	−0.78	0.44
Brood size[a]	−0.13 (±0.22)	−0.60	0.55
Sex	0.13 (±0.26)	0.49	0.63
Rank[a]	−0.13 (±0.13)	−0.99	0.32
(b) Direction of lateralization			
Food supplementation	−0.03 (±0.05)	−0.65	0.51
Brood size[a]	−0.00 (±0.04)	−0.12	0.91
Sex	−0.10 (±0.05)	−2.29	0.022
Rank[a]	−0.00 (±0.02)	−0.11	0.91

Coefficient estimates ± SE and Z-statistics are given for each fixed term in the model. The initial model included all 2-way interactions between food supplementation and other variables, and non-significant interaction terms were removed from the final model. Brood identity was included as a random term. Sample sizes: $N = 23$ nestlings from 8 control nests and $N = 38$ nestlings from 12 food-supplemented nests. [a] Estimate for mean-centered covariate.

estimate ± SE = 0.06 ± 0.03, $Z = 2.03$, $P = 0.042$, $N = 33$), whereas male nestlings showed no preference (intercept estimate ± SE = −0.05 ± 0.03, $Z = −1.40$, $P = 0.16$, $N = 28$). Brood identity did not explain any variance in the strength or the direction of lateralization (Supplementary Table S3).

There was no significant difference in body mass between nestlings in food-supplemented broods and nestlings in control broods immediately at the end of extra food provisioning (8–10 days post-hatching), but food-supplemented nestlings became significantly heavier than control nestlings at 15–16 days post-hatching (see Supplementary Table S2). Despite the positive effect of extra food provisioning on nestling body weight gain, the strength of lateralization and the direction of lateralization were not affected by food supplementation (Table 1). This result likely indicates true absence of an effect of food supplementation on lateralization in our study population rather than just a lack of statistical power because the BF indicated that the models without food supplementation as a predictor were approximately 3 times more plausible than the models including food supplementation (BF = 2.92 and BF = 3.11, for the strength and direction of lateralization, respectively).

Contrary to our predictions, we found no sex differences in the strength of nestling lateralization, independently of food supplementation (non-significant sex effect and non-significant sex × food supplementation interaction; Table 1). However, in line with results at the population level, we found that the direction of individual lateralization depended on nestling sex, as females turned their head more often toward the right compared with males (Table 1 and Figure 1). Finally, maternal body condition had no significant effect on the strength or the direction of lateralization in the offspring (Supplementary Table S6).

Discussion

Growing evidence indicates that functional specialization of the 2 sides of the brain can help individuals to cope with adverse conditions such as high predation risk and high levels of intraspecific competition or environmental stressors (Rogers 2010b; Broder and Angeloni 2014; Vila Pouca et al. 2018; Gutiérrez and Soriano-Redondo 2020). In multiple taxa, cues signaling such adverse
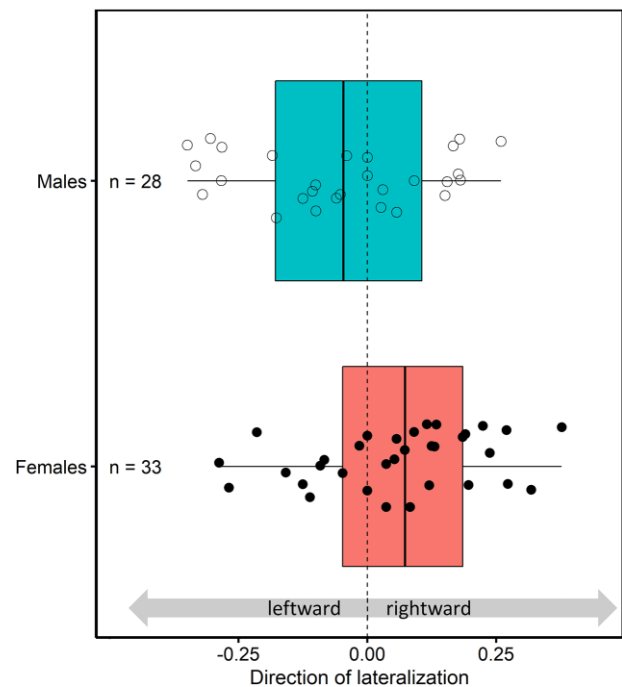

Figure 1. Direction of lateralization of preening behavior in lesser kestrel nestlings in relation to nestling sex. Sample sizes are given on the left of each box. Each box shows the group median and interquartile range. Whiskers represent the highest and lowest values and extend to a maximum of 1.5 times the interquartile range. Filled dots and orange color indicate females, empty dots, and blue color indicate males. The "n" in the figure should be italicized and capitalized, N.

conditions promote development of lateralized phenotypes through adaptive phenotypic plasticity (Broder and Angeloni 2014; Chiandetti 2017; Lucon-Xiccato et al. 2017; Dadda et al. 2020). Food shortage and competition for food could be one of the conditions in which lateralized individuals have an advantage (Dharmaretnam and Rogers 2005; Kurvers et al. 2017; Camerlink et al. 2018). However, contrary to our predictions, providing extra food from egg laying to early nestling rearing in a wild lesser kestrel population did not affect the strength of nestling lateralization for preening behavior in either males or females.

Several factors could explain why our study found no effects of extra food provisioning on nestling lateralization. First, it is possible that high natural prey abundance during the study year smoothed out differences in early rearing conditions between food-supplemented and control groups, preventing us from detecting any effect of extra food provisioning on lateralization. To our knowledge, few lateralization studies have manipulated food availability during early life (Vancassel et al. 2005; Hernandez et al. 2009; Romano et al. 2016). Of these, 2 found a change in the strength of motor lateralization in mammals following chronic undernutrition of the mother only (Hernandez et al. 2009) or both the mother and offspring (Vancassel et al. 2005). A third study in rice weevils *Sitophilus oryzae* found no differences in the direction of lateralization of mating behavior between males reared on wheat and on maize (Romano et al. 2016). Taken together, these findings suggest that the effect of food availability on the development of lateralization may only be apparent under food shortages.

Second, contrasting effects of extra food provisioning on the strength of nestling lateralization could have caused an overall null

effect. Indeed, while less stressful rearing conditions are expected to lead to lower behavioral lateralization, higher food availability during egg laying might have reduced maternal stress and hence yolk corticosterone in the egg (Saino et al. 2005; Love et al. 2008; Poisbleau et al. 2009; Schmaltz et al. 2016), favoring the development of brain lateralization in the embryos (Freire et al. 2006; Henriksen et al. 2013). However, it is worth noting that extra food provisioning started when the first egg was already laid (identifying a nest as occupied), hence a potential reduction in egg corticosterone concentration would have occurred only for eggs further down the laying sequence (i.e., lower rank nestlings), leading to an interactive effect of rank and food supplementation on the strength of nestling lateralization. This view was not supported by our data as we found no significant interaction between rank and food supplementation.

A third potential explanation is that, since nestlings showed only weak behavioral lateralization, the effect of extra food provisioning on lateralization may become apparent only in adulthood along with the establishment of patterns of motor control over the body. For example, in African gray parrots *Psittacus erithacus*, motor asymmetries become apparent only after the first month of age (Snyder and Bonner 2001). In addition, ostriches *Struthio camelus* only show a side preference for the foot used to initiate locomotion in adulthood (Baciadonna et al. 2010). Alternatively, it is also possible that extra food provisioning does not reduce nestling lateralization in the current generation but may do so in subsequent generations via epigenetic effects (Romano et al. 2015; Güntürkün and Ocklenburg 2017; Schmitz et al. 2017). For example, the greater weight gain of food-supplemented nestlings may improve body condition at fledging, which in turn predicts first-year survival and body condition in adulthood (Aparicio and Cordero 2001). Once adults, individuals with better body condition could then produce less lateralized offspring by laying eggs with different levels of maternal hormones (Groothuis et al. 2005).

Contrary to our predictions, nestling sex did not modulate the effect of extra food provisioning on the strength of nestling lateralization. However, it influenced the direction of lateralization; indeed, females showed a rightward preference at the population level but males showed no significant preference (Figure 1). A bias for head turning toward the right during preening might indicate underlying control by the contralateral left hemisphere. This would align with the role of the left hemisphere suggested by Rogers (2010b) for homeotherms, which is to "control over well-established patterns of behavior that are performed in non-stressful situations". Indeed, preening is a daily maintenance motion which is performed in the absence of threats (Spruijt et al. 1992). Such right turning preference might be less apparent in males compared with females because they might be more vulnerable to stress during rearing. In line with this explanation, in lesser kestrel fledglings, males show a stronger physiological response to stress compared with females (Ortego et al. 2009). Given that behavior in stressful situations is predominantly controlled by the right hemisphere (Ocklenburg et al. 2016; Rogers and Kaplan 2019; Mundorf et al. 2020), higher vulnerability to stress in male nestlings would increase the likelihood of developing a leftward motor bias at the individual level and explain the lack of a rightward preference at the population level in males.

Intrinsic sex differences in the development of brain lateralization provide an alternative explanation for the different direction of lateralization found in male and female nestlings. Indeed, experiments in domestic chicks have shown that males and females differ in the degree of asymmetry of visual projections (Rajendra and Rogers 1993) and its sensitivity to environmental factors, that is,

light exposure, during ontogeny (Rogers 1997, 2012). This is likely due the organizational and activational effects of sex hormones on brain development; for example, hatchlings show sexual dimorphism in the expression of sex hormone receptors in different brain regions, including the cerebellum, which controls motor coordination (Camacho-Arroyo et al. 2018). In addition, increased prenatal or postnatal testosterone promotes right hemispheric dominance versus left hemispheric dominance in domestic chicks (Pfannkuche et al. 2009) and could partly explain the lack of a rightward behavioral lateralization in males.

Our finding contributes to the complex emerging pattern of sex differences in lateralization across taxa (Ströckens et al. 2013; Niven and Frasnelli 2018). Indeed, a rightward motor preference in females and a leftward preference in males have been previously found in horses *Equus caballus* (Murphy et al. 2005), cats *Felis silvestris* (McDowell et al. 2018), and some species of primates (Milliken et al. 1991; Shaw et al. 2004; Pan et al. 2013; but see Schnoell et al. 2014; Fu et al. 2019). The proportion of individuals showing a left-hand or left-paw preference was also higher among males than females in humans (Papadatou-Pastou et al. 2008) and dogs *Canis familiaris* (Laverack et al. 2021). Additionally, female Asian tiger mosquitoes *Aedes albopictus* showed a preference for the right leg during kicking behavior (Benelli et al. 2015). However, a right limb preference was found in males of 2 species of marsupials (Giljov et al. 2013) and a right bias for head wagging behavior during courtship was found in male rice weevils (Romano et al. 2016). Therefore, future research is warranted to determine how generalizable sex differences in motor asymmetry are across taxa.

Our study adds to growing evidence of behavioral lateralization in raptors. Previous studies have reported individual- and population-level lateralization for body rotation in response to an auditory stimulus, leg use during sleep, and foot use in hunting, carrying, and handling prey, as well as preferred visual field when chasing prey, although the direction of lateralization varied with species (Palleroni and Hauser 2003; Csermely 2004; Kane and Zamani 2014; Allen et al. 2018; Yosef et al. 2019; Baciadonna et al. 2022). The only previous study investigating lateralization for preening behavior in raptors was performed on barn owls *Tyto alba* and it found that the strength of lateralization in female nestlings depended on the size of the melanic spots of the mother, an index of maternal quality (Gaillard et al. 2017). In contrast, in our study, we did not find any association between maternal quality, measured as body condition during breeding, and the strength or direction of nestling lateralization, suggesting maternal contribution to behavioral lateralization may be limited in this species.

In conclusion, to our knowledge, this is the first study that tests the influence of food availability during early life on the development of behavioral lateralization in wild birds. We measured lateralization from a spontaneous behavior after experimentally increasing food availability at the nest. Extra food provisioning did not affect the strength or direction of lateralization of preening behavior. However, we found that lateralization in female nestlings was biased to the right compared with male nestlings. Experimental manipulation of sex hormones and/or corticosterone levels in lesser kestrel eggs (prenatal) and hatchlings (postnatal) will be the next step to determine whether the observed sex difference in the direction of lateralization is better explained by a higher stress responsiveness in male nestlings or by the effects of sex hormones on brain development. Future studies could also consider different types of resource manipulation or measures of laterality. For example, manipulating brood size and/or sex ratio could be used to directly investigate the

effects of increased competition for resources on nestling laterality. Additionally, measuring turning bias in the escape response or eye dominance when looking at prey or conspecifics could represent a valid alternative to preening observations, as these measures have been previously employed to assess laterality in wild birds (e.g., Ventolini et al. 2005; Beauchamp 2013; Possenti et al. 2016) and they represent an ecologically relevant response in nestlings.

Authors' Contributions

C.S., A.B., and D.R. conceived the study. C.S., J.G.C., and D.R. collected the data. C.S. and D.R. analyzed the data. C.S. and A.B. wrote the paper with inputs from D.R. and J.G.C. All authors gave final approval for publication.

Data Statement

The data used in this study is available on Figshare, DOI: https://doi.org/10.6084/m9.figshare.19428971.v1

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Conflict of interest

All co-authors declare that they have no conflict of interests.

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