1 **Melanism is related to behavioural lateralization in**
2 **nestling barn owls**

3

4

5 Maryline Gaillard¹, Madeleine F. Scriba^{2*} & Alexandre Roulin²

6

7

8 ¹*Biogeosciences, University of Burgundy, Dijon, France*

9 ²*Department of Ecology and Evolution, University of Lausanne, Biophore Building,*

10 *CH-1015 Lausanne, Switzerland*

11

12 * Corresponding author: Madeleine.Scriba@unil.ch, Tel.: +41 76 8184285

13

14 Running title: **Melanism and laterality**

15

16 **Abstract**

17 Behavioural laterality is a commonly observed phenomenon in many species
18 suggesting there might be an advantage of using dominantly one side over the
19 other for certain tasks. Indeed, lateralized individuals were often shown to be
20 more successful in cognitive tasks compared to non-lateralized conspecifics.
21 However, stressed individuals are also often, but not always, more strongly
22 lateralized. Because barn owl (*Tyto alba*) females displaying larger black spots
23 on the tip of their ventral feathers produce offspring that are more resistant to
24 variety of environmental stressful factors, we examined whether laterality is
25 associated with melanin-based coloration. We recorded whether nestlings use
26 more often the right or left foot to scratch their body and whether they preen
27 more often one side of the body or the other using their bills. We found that the
28 strength of lateralization of preening and scratching was less pronounced in
29 individuals born from heavily spotted mothers. This result might be explained by
30 plumage-related variation in the ability to resist stressful rearing conditions.

31

32 **Keywords**

33 Bird; colouration; development; personality; preening; scratching

34

1. Introduction

Behavioural lateralization is widespread among vertebrates (Bisazza et al., 1998; Rogers & Andrew, 2002; Vallortigara et al., 2011; Rogers et al., 2013; Vallortigara & Versace, 2017) and invertebrates (Frasnelli et al., 2012; Romano, et al., 2016). It can be manifested as the preferential use of one limb over the other such as footedness in parrots (Rogers, 1989) and handedness in primates (Warren, 1980; Versace & Vallortigara, 2015). It can also concern the more frequent use of one side of sensory organs over the other side such as ear and body rotation in hawks and owls when perceiving a sound (Csermely, 2004) and visual discrimination in chickens (Rogers et al., 2004). Measuring the strength of laterality, or intensity of the preference for a specific side, is particularly important because the speed and accuracy of movements to fulfil a task are supposed to be higher when the subject uses its preferred side (Annett, 1967) conferring advantages in various types of social (Krakauer, et al., 2016), maintenance and anti-predator behaviours (Dadda & Bisazza, 2006). For instance, wild chimpanzees that use the preferred hand to extract termites with a flexible tool are more efficient in this task than non-lateralized individuals using either hand (McGrew & Marchant, 1999). However, there may be situations when a strong lateralization is disadvantageous, such as in agonistic interactions when individuals can learn and anticipate the side used by opponents (Ghirlanda & Vallortigara, 2004; Rogers et al., 2013). The benefit of a strong degree of lateralization can also be frequency-dependent (Raymond et al., 1996) and under some circumstances individuals that display the most (or least) common side preference (i.e. left- or right-hand) in the population can have a higher fitness outcome (Faurie et al., 2012). Therefore, the costs and benefits of

60 being lateralized are numerous and the identification of how inter-individual
61 variability is evolutionary stable is not trivial (Vallortigara & Rogers, 2005;
62 Ghirlanda et al., 2009).

63 The development of laterality and modulation of its expression can be
64 influenced by genetic (Suzuki & Ando, 2014; Hopkins et al., 2015) and
65 environmental factors such as early life experience (Güntürkün, 1993; Deng &
66 Rogers, 2002; Tang & Verstynen, 2002; Akers et al., 2004; Andrew et al., 2004;
67 Letzner et al., 2014), social interactions (e.g. cultural influence, stress) (Bennett
68 et al., 2008) as well as by physiological factors like hormones (Ward et al., 1990;
69 Rogers & Deng, 2005; Pfaankuche et al., 2009; Tommasi, 2009; Romano et al.,
70 2015). Many studies found that stress induces a change in the direction or
71 strength of lateralization. For instance, rats exposed to novel environments
72 during early development showed an altered paw preference compared to
73 undisturbed conspecifics (Tang & Verstynen, 2002) and sick lions (*Panthera leo*)
74 showed a stronger level of lateralization in paw preference compared to healthy
75 conspecifics (Zucca et al., 2011). In contrast, chicken (*Gallus gallus*) exposed to
76 higher corticosterone levels during egg development became less strongly
77 lateralized and more reactive to stressors (Rogers & Deng, 2005). These
78 examples show that environmental stressful factors can influence lateralization.
79 Indeed, in several species, the left hemisphere controls established patterns of
80 behaviour in non-stressful situations, whereas the right hemisphere controls
81 emergency responses and physiological stress responses (MacNeilage et al.,
82 2009; Rogers, 2010). Stressful situations might cause a shift or reorganization of
83 the information processing between the two hemispheres (Rogers, 2010;
84 Domenici et al., 2014).

Recent studies showed that the degree of melanin-based coloration, the most widespread type of colour variation in animals, is associated with the ability to resist various sources of stress (Brenner & Hearing, 2008; Ruiz-De-Castañeda et al., 2012; Trullas et al., 2007; Roulin et al., 2008), life-history strategies (Emaresi et al., 2014; Sinervo & Lively, 1996) and behaviour (Ducrest et al. 2008). It is therefore possible that weakly and strongly melanised individuals differ in the degree of lateralization. Melanin-based colouration is associated with the physiological regulation of stress probably as a consequence of the melanocortin system that regulates both melanogenesis and glucocorticoids. Because there is no reason to believe that some individuals would derive fitness benefits from being lateralized for self-maintenance behaviour such as scratching and preening, we speculate that individuals that better regulate glucocorticoid-dependent stress response are less lateralized. Lateralization has been intensely studied in birds in the context of tool or food manipulation (Izawa et al., 2005; Magat & Brown, 2009), foraging such as scratching the ground with feet (Rogers & Workman, 1993; Tommasi & Vallortigara, 1999), eye use (Ventolini et al., 2005; Hoffman et al., 2006; George et al., 2006), visual lateralization in the homing of pigeons (Prior et al., 2004), and resting posture (Randler, 2007; Anderson et al., 2009), but there is to date no data investigating the potential link between melanism and lateralization.

We carried out a study in a wild population of barn owls (*Tyto alba*) using video-recordings of nestlings in their natural nest. This species is particularly interesting because its ventral body side varies from immaculate to heavily-marked with black spots of varying size. The size of maternal spots covaries with many physiological, morphological and behavioural traits measured in their

young offspring potentially as a result of pleiotropic effects of genes involved in melanogenesis and other phenotypes (Roulin & Ducrest, 2011). The fact that nestling quality is associated more often with the diameter of black feather spots measured in mothers than in the nestling themselves suggest spottiness-related maternal effects or genomic imprinting. The finding that larger-spotted mothers produce offspring that better cope with any kind of stressful factors that induce a rise in corticosterone levels (Almasi et al., 2010; 2012), and that the amount of black feather spots is associated with behaviour (van den Brink et al. 2012; Peleg et al. 2014) and brain activity (Scriba et al. 2013; 2014) in this species raises the hypothesis that the degree of offspring lateralization may be correlated with maternal spottiness. Furthermore, mothers displaying larger black spots gave birth to offspring that developed wing feathers on the left and right wing of a more similar size than offspring born from smaller-spotted mothers (Roulin et al., 2003). We therefore tested whether the degree of lateralization in nestling barn owls is correlated with the size of maternal black feather spots. To this end, we video-recorded nestlings in their natural nest and investigated lateralization in two behaviours, preening and scratching. We investigated these behaviours because in earlier studies we found a link between melanin-based colouration and preening effort (Roulin, 2007; Roulin et al., 2016) and, furthermore, these behaviours are frequent and hence we can relatively easily monitor laterality.

2. Material and Methods

2.1 General methods

The study was performed in western Switzerland (46°49'N, 06°56'E) in a free-living population of barn owls breeding in nest-boxes fixed against the wall of

farms. We video-recorded nestling activities with an infrared sensitive camera fixed inside nest-boxes. In 1997, this was done in 13 two-chick broods during two successive nights from approximately 1h before sunset until midnight. In total, we analysed behaviour in 25 nestlings over two nights and in one individual during one night. Nestlings were aged on average 35.9 ± 5.5 days (mean $\pm$ SE; range: 23 - 47). In 2000, we video-recorded nine two-chick broods and we successfully obtained data on laterality in one chick for three nights, in one chick for two nights and in 21 chicks for one night. As in 1997, we filmed nestlings from 1h before sunset until midnight. In 2004, we video-recorded 20 two-chick broods with a total of 40 nestlings during one entire night per individual (from 1h before sunset until the early morning). Including data of all three years, each individual had been filmed during on average ($\pm$ SD) $2h40 \pm 2h13$ (range: 8 min to 8h10). Siblings were ringed on different legs to recognize their identity on video footage.

Nestling sex was identified with molecular markers using a small blood sample. Age was determined shortly after hatching by measuring the wing length (Roulin, 2004b). One person measured the diameter of black plumage spots on the breast of the nestlings and their parents. The method of assessing spot diameters is reliable with repeatabilities ranging from 0.84 to 0.92 (Roulin, 2004c).

2.2 Assessment of laterality

We considered laterality of the preening and scratching behaviours. The side of the body nestlings were preening themselves with their beak was recorded. Preening was identified in 89 nestlings on average 24.4 ± 1.8 times (range: 2 -

84). Which side of the body nestlings scratched using a foot was identified in 73 nestlings on average 10.1 ± 0.8 times (range: 2 - 32).

For each of the 89 nestling, each behaviour and across all nights (range: 1 and 3 nights, on average 1.31 nights), we summed the number of times the left or right foot for scratching and the body side for preening has been used. From these summed observations, we obtained a laterality index for each of the behaviour (i.e. the level to which nestlings are left- or right-biased) with the following formula:
$$\frac{|\text{total number of times the right side of the body was used} - \text{total number of times the left side of the body was used}|}{\text{total number of times the right side of the body was used} + \text{total number of times the left side of the body was used}}$$
. The absolute values of this index was referred to as “strength of laterality” and Box-Cox transformed to normalize the dataset. Positive values indicate a preference for the right side and negative values represent a preference for the left side.

2.3 Statistical analyses

We first examined whether nestlings were significantly left- or right-biased for preening and scratching behaviour. We only considered behaviours observed on more than nine occasions per individual giving a reliable measure of laterality as in other studies (Domenici et al., 2014; Izawa et al., 2005; Karenina et al., 2016; Magat & Brown, 2009; Reddon et al., 2009). If an individual had been observed on more than one night, we summed the observations done on these successive nights. We applied two-tailed binomial tests in each individual to test whether they were significantly lateralized. If scratching and preening have similar

function, nestlings that scratched their body more often than other individuals should also preen it more frequently. We used Pearson's correlation to test if preening and scratching were related.

We then used linear mixed models with the laterality index values or Box-Cox transformed strength of laterality as dependent variable. The nest of origin and year were included as random variables to control for relatedness between individuals from the same nest. Age, sex, and plumage spottiness of parents or nestlings were included as fixed effects into the models. In preliminary analyses, the two random variables explained a weak part of the variation ($< 8\%$) and were removed from the analyses. Keeping these random variables did not modify our conclusions. We log-transformed the number of times behaviours were observed to obtain a normal distribution and to test if the sample size had an effect on the dependent variables, using it as a fixed effect. *P*-values smaller than 0.05 were considered significant. Statistical analyses were performed with the software JMP (version 11.0, SAS Institute Inc., Cary, NC).

3. Results

Across all 89 individuals, nestlings preened the right side of the body (mean $\pm$ standard deviation: $48.4\% \pm 12.4\%$) less often than the left side (Wilcoxon matched-pair signed rank: $S = -1057.5$, $P < 0.0001$) and they scratched the right side of the body more often (mean $\pm$ standard deviation: $52.6\% \pm 21.7\%$) than the left side (46.0% ; $S = 506.50$, $P = 0.038$). In 32 individuals, we observed scratching more than 9 times and from these birds, 3 used significantly the right side more often than the left side as shown by binomial tests. In 75 birds, we recorded preening more than 9 times and found 6 lateralized nestlings: 2 birds

209 preened the right side more frequently than the left side and 4 birds preened the
 210 left side more frequently than the right side (binomial test). Within individuals,
 211 birds that scratch the right side of the body were also more likely to preen this
 212 side ($r = 0.29$, $n = 78$, $P = 0.009$). Because scratching and preening the body are
 213 positively correlated and serve the same function, for each individual we
 214 summed the number of times these two behaviours were performed on each side
 215 of the body. From 89 individuals, 84 performed scratching or preening at least 9
 216 times. In a preliminary linear mixed model, the random variables “nest of origin”
 217 and “year” (explaining less than 6.7% of the variation) as well as the factor
 218 “nestling age” ($F_{1,49.87} = 0.08$, $P = 0.77$) did not explain any part of the variation
 219 and hence were removed from the model. The Box-Cox transformed strength of
 220 laterality was strongly related to the interaction between nestling sex and
 221 maternal spot diameter (maternal spot diameter: $F_{1,80} = 1.32$, $P = 0.25$; sex: $F_{1,80} =$
 222 0.05 , $P = 0.82$; interaction: $F_{1,80} = 7.44$, $P = 0.0078$; similar analyses using the
 223 laterality index, on whether offspring born from larger-spotted mothers preen
 224 and scratch more one side of the body than the other side compared to offspring
 225 born from smaller-spotted mothers gave non-significant results, all P -values $>$
 226 0.28). The interaction was significant, because in nestling females the strength of
 227 laterality was more pronounced if their mother displayed larger black spots
 228 (Pearson’s correlation: $r = -0.41$, $n = 41$, $P = 0.0081$; Figure 1), whereas in male
 229 nestlings there was no association ($r = 0.02$, $n = 26$, $P = 0.93$). When calculating a
 230 mean value for each biological mother, the strength of laterality in nestling
 231 females was still significantly associated with maternal spot diameter (Pearson’s
 232 correlation: $r = -0.52$, $n = 31$, $P = 0.0029$). When we replaced maternal spot
 233 diameter with spot diameter measured in the nestling themselves ($r = -0.25$, $n =$

35, $P = 0.14$) or in the father ($r = -0.15$, $n = 38$, $P = 0.36$), the covariations were not significant. Although the log-transformed sample size (i.e. the number of times behaviours were observed) was negatively correlated with the strength of laterality ($r = -0.22$, $n = 99$, $P = 0.026$) and could have biased our results, adding this variable as fixed effect did not modify our conclusion: the interaction of maternal spot diameter and sex was still significant ($F_{1,79} = 8.48$, $P = 0.0047$).

4. Discussion

Although the present study shows that in nestling barn owls, very few individuals were significantly lateralized for preening and scratching the body (3 out of 32 individuals for scratching and 6 out of 75 individuals for preening), the strength of lateralization was less pronounced in offspring born from heavily spotted mothers compared to weakly spotted mothers.

We found inter-individual variation in the preference of the side used with the foot and head, with some individuals being significantly lateralized (9% of the birds were lateralized for scratching and 8% of the birds for preening). In other studies on birds, the number of individuals showing side preferences varied remarkably between studies. For example, 11 out of 13 jungle-crows (86%) (*Corvus macrorhynchos*) used one foot more frequently than the other to scratch the beak (6 preferred the left side and 5 the right side) and 10 out of 12 subjects (83%) preferred holding food with one foot (5 individuals preferred the left foot and 5 the right foot) (Izawa et al., 2005). From 17 Caribbean flamingos (*Phoenicopterus ruber*), 5 individuals (29%) placed their head on one side of the body preferentially over the other side during rest (Anderson et al., 2009). All 10 observed New Caledonian crows (*Corvus moneduloides*) showed laterality in the

side they hold the stick with their beak when extracting food (5 individuals preferred the left side and 5 the right one) (Weir et al., 2004).

Assuming that it takes time to learn which side of the body is the most efficient, nestlings may not have sufficient experience to already show a preferential use of one limb. For instance, marmosets (*Callithrix jacchus*) do not have a significant preference for using one hand over the other in uni-manual holding before five months of age, the time when they start to hold food with one specific hand (Hook & Rogers, 2000). Nestling African grey parrots (*Psittacus erithacus*) did not show lateralization before 23 days of age, but from day 29 onwards they showed consistent left postural and motor asymmetry (Snyder & Bonner, 2001). Another example is in California sea lions (*Zalophus californianus*) and rhesus monkeys (*Macaca mulatta*) in which lateralisation in head turning was not detected in young individuals, but in adults (Böye et al., 2005; Hauser & Andersson, 1994). These studies indicate that a lateral use of one side of the body might depend on the maturation of neural control over the body, on gained experience or on the time required to practice activities with only one side of the body. In the case of the barn owl, only few individuals showed significant preference of one side of the body, perhaps because strong lateralization appears mainly in experienced individuals. Even if we did not find evidence for a correlation between the strength of laterality and nestling age, we cannot exclude that more individuals show lateralization only at adulthood.

We found a link between the strength of laterality and the eumelanic coloration of the mother. Mothers displaying larger black feather spots produced offspring that were less intensely lateralized for preening and scratching the body. Nestlings from heavily spotted mothers do better on a variety of

phenotypic traits, than those of lightly spotted mothers including the regulation of corticosterone, immunity and energy homeostasis (Roulin & Ducrest, 2011). Interestingly, Roulin et al. (2003) showed that individuals from females with bigger spots are more symmetric in their body morphology. Behavioural laterality may be triggered by the body asymmetry due to perturbations during development (loss of genetic variation or environmental stress; Leary & Allendorf, 1989; Hopkins et al., 2001). Therefore, body symmetry and a lack of behavioural lateralization might indicate phenotypic quality as those individuals may be better in maintaining normal growth during environmental perturbations (e.g. Hopkins et al., 2001). Barn owls born from lightly spotted mothers that are less symmetrical may have developed a stronger lateralization. Barn owls, which are morphologically lateralized, might have an advantage due to the resulting behavioural lateralization, but the behavioural lateralization might as well be a compensation for the potentially disadvantageous morphological asymmetry. The different phenotypes might use different strategies to maximise fitness – body symmetry or behavioural laterality. This interpretation would also be consistent with the fact that larger spotted females produce offspring that are better able to regulate blood-circulating corticosterone (Almasi et al., 2012). Indeed, the principal stress hormone in birds, corticosterone, also modulates the development of lateralization in the visual pathways, as shown in chicken (Rogers & Deng, 2005). Chicken (*Gallus gallus*) with artificially elevated levels of corticosterone in the egg become more reactive to stressors and less strongly lateralized showing fewer projections from the left side of the thalamus to the right Wulst compared to control chickens (Rogers & Deng, 2005).

Some studies suggest that lateralization is linked to personality traits with strongly lateralized individuals being bolder and more risk-taking compared to less lateralized individuals which behave more cautiously and are risk-averse (Reddon & Hurd, 2009). This link might be the direct result of the symmetric or asymmetric processing of information in the two brain hemispheres. Less lateralized individuals might take more time to react, as the consensus-making process relies on a consensus of the two hemispheres. In strongly lateralized individuals, the dominant hemisphere for a given function will override actions from the other hemisphere, thereby increasing the efficiency of a decision and action (Reddon & Hurd, 2009). Darker eumelanic barn owl nestlings were shown to be more docile when handled, hissed more intensely and feigned death longer in the presence of humans, suggesting a more passive anti-predator strategy (Peleg et al., 2014; van den Brink et al., 2012). In contrast, nestlings with small black spots appeared to be particularly bold as they were physically more aggressive and agitated when handled. Furthermore, nestlings born from darker eumelanic mothers switch more frequently between wakefulness and sleep leading to increased vigilance in sibling competition (Scriba et al., 2014). This shows that different behavioural and physiological strategies connected to melanin-based coloration exist which might be linked to lateralized behaviour. Further support for this idea comes from studies in two different populations of poeciliid fish exposed to different predation pressures, which showed differences in laterality and personality traits (Brown et al., 2005; 2007), as well as a study showing links between aggressiveness and laterality in cichlid fish (Reddon & Hurd, 2008).

Acknowledgements

The study was supported by the Swiss National Science Foundation 31003A-120517 to AR. We are grateful to Olga Lazareva and two anonymous reviewers for helpful comments on a previous version of the manuscript.

Ethical approval

This research adhered to the National Institutes of Health standards regarding the care and use of animals in research. All protocols were approved by the Service Vétérinaire du Canton de Vaud.

Literature Cited

- Akers, K. G., Reeb, B. C., & Tang, A. C. (2004). Developmentally stable sex-dependent modulation of turning asymmetry by neonatal novelty exposure. *Behavioural brain research*, 155(2), 257-263.
- Almasi, B., Jenni, L., Jenni-Eiermann, S., & Roulin, A. (2010). Regulation of stress response is heritable and functionally linked to melanin-based coloration. *Journal of Evolutionary Biology*, 23, 987-996. <http://doi.org/10.1111/j.1420-9101.2010.01969.x>
- Almasi, B., Roulin, A., Korner-Nievergelt, F., Jenni-Eiermann, S., & Jenni, L. (2012). Coloration signals the ability to cope with elevated stress hormones: effects of corticosterone on growth of barn owls are associated with melanism: Plumage coloration and stress sensitivity. *Journal of Evolutionary Biology*, 25, 1189-1199. <http://doi.org/10.1111/j.1420-9101.2012.02508.x>
- Anderson, M. J., Williams, S. A., & O'Brien, E. H. (2009). Individual differences in the preferred neck-resting position of Caribbean flamingos (*Phoenicopterus ruber*). *Laterality: Asymmetries of Body, Brain and Cognition*, 14, 66-78. <http://doi.org/10.1080/13576500802233722>
- Andrew, R. J., Johnston, A. N. B., Robins, A. & Rogers, L. J. (2004). Light experience and the development of behavioural lateralization in chicks: II. Choice of familiar versus unfamiliar model social partner. *Behavioural Brain Research*, 155, 67-76.

- 365 Annett, M. (1967). The binomial distribution of right, mixed and left handedness.
 366 *Quarterly Journal of Experimental Psychology*, 19, 327–333.
 367 <http://doi.org/10.1080/14640746708400109>
- 368 Bennett, A. J., Suomi, S. J., & Hopkins, W. D. (2008). Effects of early adverse
 369 experiences on behavioural lateralisation in rhesus monkeys (*Macaca*
 370 *mulatta*). *Laterality*, 13(3), 282-292.
- 371 Bisazza, A., Rogers, L. J., & Vallortigara, G. (1998). The origins of cerebral
 372 asymmetry: a review of evidence of behavioural and brain lateralization in
 373 fishes, reptiles and amphibians. *Neuroscience & Biobehavioral Reviews*, 22,
 374 411–426.
- 375 Böye, M., Güntürkün, O., & Vauclair, J. (2005). Right ear advantage for conspecific
 376 calls in adults and subadults, but not infants, California sea lions (*Zalophus*
 377 *californianus*): hemispheric specialization for communication?. *European*
 378 *Journal of Neuroscience*, 21(6), 1727-1732.
- 379 Branson, N. J., & Rogers, L. J. (2006). Relationship between paw preference
 380 strength and noise phobia in *Canis familiaris*. *Journal of Comparative*
 381 *Psychology*, 120(3), 176.
- 382 Brenner, M., & Hearing, V.J. (2008) The protective role of melanin against UV
 383 damage in human skin. *Photochem. Photobiol.* 84, 539–549.
- 384 Brown, C., Jones, F. & Braithwaite, V. 2005 In situ examination of boldness–
 385 shyness traits in the tropical poeciliid, *Brachyrhaphis episcopi*. *Anim. Behav.*
 386 70, 1003–1009. doi:10.1016/j.anbehav.2004.12.022
- 387 Brown, C., Western, J., & Braithwaite, V. A. (2007). The influence of early
 388 experience on, and inheritance of, cerebral lateralization. *Animal Behaviour*,
 389 74, 231–238. <http://doi.org/10.1016/j.anbehav.2006.08.014>
- 390 Corballis, M. C. (2009). The evolution and genetics of cerebral asymmetry.
 391 *Philosophical Transactions of the Royal Society of London B: Biological*
 392 *Sciences*, 364(1519), 867-879.
- 393 Csermely, D. (2004). Lateralisation in birds of prey: adaptive and phylogenetic
 394 considerations. *Behavioural Processes*, 67, 511–520.
 395 <http://doi.org/10.1016/j.beproc.2004.08.008>
- 396 Dadda, M., & Bisazza, A. (2006). Does brain asymmetry allow efficient
 397 performance of simultaneous tasks? *Animal Behaviour*, 72, 523–529.
 398 <http://doi.org/10.1016/j.anbehav.2005.10.019>

- 399 Deng, C. & Rogers, L. J. (2002). Prehatching visual experience and lateralization
400 in the visual Wulst of the chick. *Behavioural Brain Research*, 134, 375–85.
- 401 Domenici, P., Allan, B. J. M., Watson, S.-A., McCormick, M. I., & Munday, P. L.
402 (2014). Shifting from Right to Left: The Combined Effect of Elevated CO₂ and
403 Temperature on Behavioural Lateralization in a Coral Reef Fish. *PLoS ONE*, 9.
404 <http://doi.org/10.1371/journal.pone.0087969>
- 405 Emaresi, G., Bize, P., Altwegg, R., Henry, I., van den Brink, V., Gasparini, J., Roulin,
406 A. (2014). Melanin-specific life history strategies. *American Naturalist*, 183,
407 269-280.
- 408 Faurie, C., Llaurens, V., Hegay, T., & Raymond, M. (2012). Handedness and
409 socioeconomic status in an urban population in Uzbekistan. *Evolution and*
410 *Human Behavior*, 33, 35–41.
411 <http://doi.org/10.1016/j.evolhumbehav.2011.05.003>
- 412 Frasnelli, E., Vallortigara, G., & Rogers, L. J. (2012). Left–right asymmetries of
413 behaviour and nervous system in invertebrates. *Neuroscience &*
414 *Biobehavioral Reviews*, 36, 1273–1291.
415 <http://doi.org/10.1016/j.neubiorev.2012.02.006>
- 416 George, I., Hara, E., & Hessler, N. A. (2006). Behavioral and neural lateralization
417 of vision in courtship singing of the zebra finch. *Journal of Neurobiology*, 66,
418 1164–1173. <http://doi.org/10.1002/neu.20273>
- 419 Ghirlanda, S., Frasnelli, E., & Vallortigara, G. (2009). Intraspecific competition and
420 coordination in the evolution of lateralization. *Philosophical Transactions of*
421 *the Royal Society of London B: Biological Sciences*, 364(1519), 861-866.
- 422 Ghirlanda, S., & Vallortigara, G. (2004). The evolution of brain lateralization: a
423 game-theoretical analysis of population structure. *Proceedings of the Royal*
424 *Society of London-B*, 271, 853–858.
- 425 Gonzalez, S. L., & Nelson, E. L. (2015). Addressing the gap: a blueprint for
426 studying bimanual hand preference in infants. *Frontiers in psychology*, 6, 560.
427 <http://doi.org/10.3389/fpsyg.2015.00560>
- 428 Güntürkün, O. (1993) The ontogeny of visual lateralization in pigeons. *German*
429 *Journal of Psychology*, 17, 276–87.
- 430 Güntürkün, O., Diekamp, B., Manns, M., Nottelmann, F., Prior, H., Schwarz, A., &
431 Skiba, M. (2000). Asymmetry pays: visual lateralization improves
432 discrimination success in pigeons. *Current Biology*, 10, 1079–1081.

- 433 Hauser, M. D., & Andersson, K. (1994). Left hemisphere dominance for
434 processing vocalizations in adult, but not infant, rhesus monkeys: field
435 experiments. *Proceedings of the National Academy of Sciences*, 91(9), 3946-
436 3948.
- 437 Hoffman, A. M., Robakiewicz, P. E., Tuttle, E. M., & Rogers, L. J. (2006).
438 Behavioural lateralisation in the Australian magpie (*Gymnorhina tibicen*).
439 *Laterality: Asymmetries of Body, Brain and Cognition*, 11, 110–121.
440 <http://doi.org/10.1080/13576500500376674>
- 441 Hopkins, W. D. (2013a). Comparing human and nonhuman primate handedness:
442 challenges and a modest proposal for consensus. *Dev. Psychobiol.*, 55, 621–
443 636. <http://doi.org/10.1002/dev.21139>
- 444 Hopkins, W. D. (2013b). Independence of data points in the measurement of
445 hand preferences in primates: Statistical problem or urban myth?: Assessing
446 Handedness in Nonhuman Primates. *American Journal of Physical*
447 *Anthropology*, 151, 151–157. <http://doi.org/10.1002/ajpa.22248>
- 448 Hopkins, W. D., Dahl, J. F., & Pilcher, D. (2001). Genetic influence on the
449 expression of hand preferences in chimpanzees (*Pan troglodytes*): Evidence
450 in support of the right-shift theory and developmental instability.
451 *Psychological Science*, 12(4), 299–303.
- 452 Hopkins, W. D., Reamer, L., Mareno, M. C., & Schapiro, S. J. (2015). Genetic basis in
453 motor skill and hand preference for tool use in chimpanzees (*Pan*
454 *troglodytes*). *Proceedings of the Royal Society of London B: Biological Sciences*,
455 282, 20141223. <http://doi.org/10.1098/rspb.2014.1223>
- 456 Hook, M. A., & Rogers, L. J. (2000). Development of hand preferences in
457 marmosets (*Callithrix jacchus*) and effects of aging. *Journal of Comparative*
458 *Psychology*, 114, 263.
- 459 Izawa, E.-I., Kusayama, T., & Watanabe, S. (2005). Foot-use laterality in the
460 Japanese jungle crow (*Corvus macrorhynchos*). *Behavioural Processes*, 69,
461 357–362. <http://doi.org/10.1016/j.beproc.2005.02.001>
- 462 Karenina, K., Giljov, A., Ivkovich, T., & Malashichev, Y. (2016). Evidence for the
463 perceptual origin of right-sided feeding biases in cetaceans. *Animal*
464 *Cognition*, 19, 239–243. <http://doi.org/10.1007/s10071-015-0899-4>
- 465 Krakauer, A. H., Blundell, M. A., Scanlan, T. N., Wechsler, M. S., McCloskey, E. A.,
466 Yu, J. H., & Patricelli, G. L. (2016). Successfully mating male sage-grouse show
467 greater laterality in courtship and aggressive interactions. *Animal Behaviour*,
468 111, 261–267. <http://doi.org/10.1016/j.anbehav.2015.10.031>

- 469 Leary, R. F., & Allendorf, F. W. (1989). Fluctuating asymmetry as an indicator of
470 stress: Implications for conservation biology. *Trends in Ecology & Evolution*,
471 4, 214–217. [http://doi.org/10.1016/0169-5347\(89\)90077-3](http://doi.org/10.1016/0169-5347(89)90077-3)
- 472 Letzner, S., Patzke, N., Verhaal, J., & Manns, M. (2014). Shaping a lateralized brain:
473 asymmetrical light experience modulates access to visual interhemispheric
474 information in pigeons. *Scientific reports*, 4, 4253.
- 475 MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Origins of the left & right
476 brain. *Scientific American*, 301(1), 60-67.
- 477 Magat, M., & Brown, C. (2009). Laterality enhances cognition in Australian
478 parrots. *Proceedings of the Royal Society B: Biological Sciences*, 276, 4155–
479 4162. <http://doi.org/10.1098/rspb.2009.1397>
- 480 McGrew, W. C., & Marchant, L. F. (1999). Laterality of hand use pays off in
481 foraging success for wild chimpanzees. *Primates*, 40, 509–513.
- 482 Nelson, E. L., Figueroa, A., Albright, S. N., & Gonzalez, M. F. (2015). Evaluating
483 handedness measures in spider monkeys. *Animal cognition*, 18(1), 345-353.
- 484 Peleg, O., Charter, M., Leshem, Y., Izhaki, I., & Roulin, A. (2014). Conditional
485 association between melanism and personality in Israeli Barn Owls. *Bird*
486 *Study*, 61(4), 572-577.
- 487 Pfannkuche, K. A., Bouma, A., & Groothuis, T. G. (2009). Does testosterone affect
488 lateralization of brain and behaviour? A meta-analysis in humans and other
489 animal species. *Philosophical Transactions of the Royal Society B: Biological*
490 *Sciences*, 364, 929–942. <http://doi.org/10.1098/rstb.2008.0282>
- 491 Piddington, T., & Rogers, L. J. (2013). Strength of hand preference and dual task
492 performance by common marmosets. *Animal cognition*, 16(1), 127-135.
- 493 Prior, H., Wiltschko, R., Stapput, K., Güntürkün, O., & Wiltschko, W. (2004). Visual
494 lateralization and homing in pigeons. *Behavioural Brain Research*, 154, 301–
495 310. <http://doi.org/10.1016/j.bbr.2004.02.018>
- 496 Randler, C. (2007). Foot preferences during resting in wildfowl and waders.
497 *Laterality: Asymmetries of Body, Brain and Cognition*, 12, 191–197.
498 <http://doi.org/10.1080/13576500601005776>
- 499 Raymond, M., Pontier, D., Dufour, A.-B., & Møller, A. P. (1996). Frequency-
500 Dependent Maintenance of Left Handedness in Humans. *Proceedings of the*
501 *Royal Society B: Biological Sciences*, 263, 1627–1633.
502 <http://doi.org/10.1098/rspb.1996.0238>

- 503 Reddon, A. R., Gutiérrez-Ibáñez, C., Wylie, D. R., & Hurd, P. L. (2009). The
504 relationship between growth, brain asymmetry and behavioural
505 lateralization in a cichlid fish. *Behavioural Brain Research*, 201, 223–228.
506 <http://doi.org/10.1016/j.bbr.2009.02.015>
- 507 Reddon, A. R., & Hurd, P. L. (2008). Aggression, sex and individual differences in
508 cerebral lateralization in a cichlid fish. *Biology Letters*, 4(4), 338–340.
509 <http://doi.org/10.1098/rsbl.2008.0206>
- 510 Reddon, A. R., & Hurd, P. L. (2009). Acting unilaterally: Why do animals with
511 strongly lateralized brains behave differently than those with weakly
512 lateralized brains?. *Bioscience Hypotheses*, 2(6), 383–387.
- 513 Rogers, L. J. (1989). Laterality in animals. *International Journal of Comparative*
514 *Psychology*, 3(1).
- 515 Rogers, L. J. (2010). Relevance of brain and behavioural lateralization to animal
516 welfare. *Applied Animal Behaviour Science*, 127(1), 1–11.
- 517 Rogers, L. J., & Andrew, R. (2002). *Comparative Vertebrate Lateralization*.
518 Cambridge, U.K.: University Press.
- 519 Rogers, L. J., & Deng, C. (2005). Corticosterone treatment of the chick embryo
520 affects light-stimulated development of the thalamofugal visual pathway.
521 *Behavioural Brain Research*, 159, 63–71.
522 <http://doi.org/10.1016/j.bbr.2004.10.003>
- 523 Rogers, L. J., Vallortigara, G., & Andrew, R. J. (2013). Divided brains: the biology
524 and behaviour of brain asymmetries. Cambridge University Press.
- 525 Rogers, L. J., & Workman, L. (1993). Footedness in birds. *Animal Behaviour*, 45,
526 409–411. <http://doi.org/10.1006/anbe.1993.1049>
- 527 Rogers, L. J., Zucca, P., & Vallortigara, G. (2004). Advantages of having a
528 lateralized brain. *Proceedings of the Royal Society of London B: Biological*
529 *Sciences*, 271, S420–S422.
- 530 Romano, D., Donati, E., Canale, A., Messing, R. H., Benelli, G., & Stefanini, C. (2016).
531 Lateralized courtship in a parasitic wasp. *Laterality: Asymmetries of Body,*
532 *Brain and Cognition*, 21, 243–254.
533 <http://doi.org/10.1080/1357650X.2016.1150289>
- 534 Romano, M., Parolini, M., Caprioli, M., Spiezio, C., Rubolini, D., & Saino, N. (2015).
535 Individual and population-level sex-dependent lateralization in yellow-
536 legged gull (*Larus michahellis*) chicks. *Behavioural Processes*, 115, 109–116.
537 <http://doi.org/10.1016/j.beproc.2015.03.012>

- 538 Roulin, A. (2004b). The function of food stores in bird nests: observations and
539 experiments in the barn owl *Tyto alba*. *Ardea*, 92, 69–78.
- 540 Roulin, A. (2004c). Proximate basis of the covariation between a melanin-based
541 female ornament and offspring quality. *Oecologia*, 140, 668–675.
542 <http://doi.org/10.1007/s00442-004-1636-x>
- 543 Roulin, A. (2007). Melanin pigmentation negatively correlates with plumage
544 preening effort in barn owls. *Functional Ecology*, 21, 264–271.
- 545 Roulin, A., des Monstiers, B., Ifrid, E., Da Silva, A., Genzoni, E., & Dreiss, A.N.
546 (2016). Reciprocal preening and food sharing in colour polymorphic nestling
547 barn owls. *Journal of Evolutionary Biology*, 29, 380–394.
- 548 Roulin, A., & Ducrest, A.-L. (2011). Association between melanism, physiology
549 and behaviour: A role for the melanocortin system. *European Journal of*
550 *Pharmacology*, 660, 226–233. <http://doi.org/10.1016/j.ejphar.2011.01.036>
- 551 Roulin, A., Ducrest, A.-L., Balloux, F., Dijkstra, C., & Riols, C. (2003). A female
552 melanin ornament signals offspring fluctuating asymmetry in the barn owl.
553 *Proceedings of the Royal Society of London B: Biological Sciences*, 270, 167–
554 171.
- 555 Roulin, A., Gasparini, J., Bize, P., Ritschard, M., & Richner, H. (2008). Melanin-
556 based colorations signal strategies to cope with poor and rich environments.
557 *Behavioral Ecology and Sociobiology*, 62, 507–519.
- 558 Ruiz-De-Castañeda, R., Burt, J., Edward, H., González-Braojos, S., & Moreno, J.
559 (2012). Bacterial degradability of an intrafeather unmelanized ornament: a
560 role for feather-degrading bacteria in sexual selection?. *Biological Journal of*
561 *the Linnean Society*, 105(2), 409–419.
- 562 Scriba, M. F., Ducrest, A. L., Henry, I., Vyssotski, A. L., Rattenborg, N. C., & Roulin,
563 A. (2013). Linking melanism to brain development: expression of a
564 melanism-related gene in barn owl feather follicles covaries with sleep
565 ontogeny. *Frontiers in zoology*, 10(1), 42.
- 566 Scriba, M. F., Rattenborg, N. C., Dreiss, A. N., Vyssotski, A. L., & Roulin, A. (2014).
567 Sleep and vigilance linked to melanism in wild barn owls. *Journal of*
568 *evolutionary biology*, 27(10), 2057–2068.
- 569 Sinervo, B., & Lively, C. M. (1996). The rock-paper-scissors game and the
570 evolution of alternative male strategies. *Nature*, 380(6571), 240.

- 571 Snyder, P. J., & Bonner, J. A. (2001). Postnatal development of lateralized motor
572 preference in the African Grey parrot (*Psittacus erithacus*). *Brain and*
573 *cognition*, 46(1), 276-279.
- 574 Suzuki, K., & Ando, J. (2014). Genetic and environmental structure of individual
575 differences in hand, foot, and ear preferences: A twin study. *Laterality:*
576 *Asymmetries of Body, Brain and Cognition*, 19(1), 113-128.
- 577 Tang, A. C., & Verstynen, T. (2002). Early life environment modulates
578 'handedness' in rats. *Behavioural brain research*, 131(1), 1-7.
- 579 Tommasi, L. (2009). Mechanisms and functions of brain and behavioural
580 asymmetries. *Philosophical Transactions of the Royal Society B: Biological*
581 *Sciences*, 364, 855-859. <http://doi.org/10.1098/rstb.2008.0293>
- 582 Tommasi, L., Vallortigara, G. (1999). Footedness in binocular and monocular chicks.
583 *Laterality*, 4, 89-95.
- 584 Trullas, S. C., van Wyk, J. H., & Spotila, J. R. (2007). Thermal melanism in
585 ectotherms. *Journal of Thermal Biology*, 32(5), 235-245.
- 586 van den Brink, V., Dolivo, V., Falourd, X., Dreiss, A. N., & Roulin, A. (2012). Melanic
587 color-dependent antipredator behavior strategies in barn owl nestlings.
588 *Behavioral Ecology*, 23(3), 473-480.
- 589 Vallortigara, G., Chiandetti, C., & Sovrano, V. A. (2011). Brain asymmetry
590 (animal). *Wiley Interdisciplinary Reviews: Cognitive Science*, 2, 146-157.
591 <http://doi.org/10.1002/wcs.100>
- 592 Vallortigara, G. & Rogers, L.J. (2005) Survival with an asymmetrical brain:
593 advantages and disadvantages of cerebral lateralization. *Behavioral and*
594 *Brain Sciences*, 28, 575-633.
- 595 Vallortigara, G., Versace, E. (2017). Laterality at the Neural, Cognitive, and
596 Behavioral Levels. In "APA Handbook of Comparative Psychology: Vol. 1.
597 Basic Concepts, Methods, Neural Substrate, and Behavior", J. Call (Editor-in-
598 Chief), pp. 557-577, American Psychological Association, Washington DC.
- 599 Ventolini, N., Ferrero, E. A., Sponza, S., Della Chiesa, A., Zucca, P., & Vallortigara, G.
600 (2005). Laterality in the wild: preferential hemifield use during predatory
601 and sexual behaviour in the black-winged stilt. *Animal Behaviour*, 69, 1077-
602 1084. <http://doi.org/10.1016/j.anbehav.2004.09.003>
- 603 Versace, E., Vallortigara, G. (2015). Forelimb preferences in human beings and
604 other species: multiple models for testing hypotheses on lateralization.
605 *Frontiers in Psychology*, 6, 233. <http://doi.org/10.3389/fpsyg.2015.00233>

- 606 Ward, J. P., Milliken, G. W., Dodson, D. L., Stafford, D. K., & Wallace, M. (1990).
 607 Handedness as a function of sex and age in a large population of *Lemur*.
 608 *Journal of Comparative Psychology*, 104, 167-173.
 609 <http://dx.doi.org/10.1037/0735-7036.104.2.167>
- 610 Warren, J. M. (1980). Handedness and laterality in humans and other animals.
 611 *Physiological Psychology*, 8, 351-359.
- 612 Weir, A. A., Kenward, B., Chappell, J., & Kacelnik, A. (2004). Lateralization of tool
 613 use in New Caledonian crows (*Corvus moneduloides*). *Proceedings of the*
 614 *Royal Society of London B: Biological Sciences*, 271(Suppl 5), S344-S346.
- 615 Zhao, D., Wang, Y., & Wei, X. (2016). Hand preference during bimanual
 616 coordinated task in northern pig-tailed macaques *Macaca leonina*. *Current*
 617 *Zoology*, zow064.
- 618 Zucca, P., Baciadonna, L., Masci, S., & Mariscoli, M. (2011). Illness as a source of
 619 variation of laterality in lions (*Panthera leo*). *Laterality: Asymmetries of Body,*
 620 *Brain and Cognition*, 16:3, 356-366, DOI: 10.1080/13576501003690025
 621

Figure 1. Strength of laterality (Box-Cox transformed) in preening and scratching behaviour in female nestling barn owls in relation to the diameter of black feather spots measured in their biological mother (Pearson's correlation: $r = -0.52$, $n = 31$, $P = 0.0029$). Each data point represents a mean nest value so that each mother appears only once.