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1 **Light enough to travel or wise enough to stay? Brain size evolution and migratory**
2 **behaviour in birds**

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10

11 **RUNNING HEAD:** Brain size evolution and migration in birds

12 **KEY WORDS:** Migration, cognition, behavioural flexibility, energy trade-off, innovation

13 **DATA ARCHIVING:** All data used is included in Supplementary Material S4

14 **Abstract**

15 Brain size relative to body size is smaller in migratory than in non-migratory birds. Two mutually non-
16 exclusive hypotheses had been proposed to explain this association. On the one hand, the ‘energetic
17 trade-off hypothesis’ claims that migratory species were selected to have smaller brains because of the
18 interplay between neural tissue volume and migratory flight. In contrast, the ‘behavioural flexibility
19 hypothesis’ argues that resident species are selected to have higher cognitive capacities, and therefore
20 larger brains, to enable survival in harsh winters, or to deal with environmental seasonality. Here, I test
21 the validity and setting of these two hypotheses using 1,466 globally distributed bird species. First, I
22 show that the negative association between migration distance and relative brain size is very robust
23 across species and phylogeny. Second, I provide strong support for the energetic trade-off hypothesis,
24 by showing the validity of the trade-off among long-distance migratory species alone. Third, using
25 resident and short-distance migratory species, I demonstrate that environmental harshness is associated
26 with enlarged relative brain size, therefore arguably better cognition. My study provides the strongest
27 comparative support to date for both the energetic trade-off and the behavioural flexibility hypotheses,
28 and highlights that both mechanisms contribute to brain size evolution, but on different ends of the
29 migratory spectrum.

30 **Introduction**

31 Brain size relative to body size has long been considered a major determinant of the cognitive abilities
32 of a given individual, or species (Sol 2009). For instance, large relative brain size has been linked to a
33 wide range of benefits, including increased survival, adaptability to novel environments, innovation
34 propensity, variability of habitats occupied, invasiveness and sociability (Lefebvre et al. 2004, Lefebvre
35 and Sol 2008, Sol 2009, Sol et al. 2007, 2010, Lefebvre 2013). Nevertheless, in spite of the
36 multifaceted benefits conferred by a large brain (relative to body size), there is a downside: high
37 metabolic cost (Sol 2009, Isler and van Schaik 2009). The brain is one of the most energetically
38 expensive organs in the body, consuming up to ten times more energy per unit mass than skeletal
39 muscle (Isler and van Schaik 2006, 2009). Therefore, relative brain size in a given species should
40 reflect a careful balance between costs and benefits; the evolutionary optimum should be the size that
41 maximises survival and reproductive success as a function of species ecology, life history, and
42 behaviour (Sol et al. 2010).

43

44 One major ecological constraint on relative brain size across flying homothermic vertebrates is distance
45 travelled during migration (Winkler et al. 2004). This association has repeatedly been demonstrated at
46 the species level in birds (e.g. Winkler et al. 2004, Sol et al. 2005, Vincze et al. 2015), and bats
47 (McGuire and Ratcliffe 2011), as well as at the subspecies level in birds (Cristol et al. 2003,
48 Pravosudov et al. 2007, Fuchs et al. 2015). The correlation is very robust and, in all cases, relative total
49 brain weight decreases with increasing migration distance (Cristol et al. 2003, Winkler et al. 2004, Sol
50 et al. 2005, Pravosudov et al. 2007, McGuire and Ratcliffe 2011, Vincze et al. 2015). The two
51 hypotheses proposed to explain this association are, by definition, explaining variation on two different
52 ends of the migratory distance spectrum (i.e. residents vs. long-distance migrants). The energetic trade-
53 off hypothesis builds upon the metabolic costs of migration, and that of developing and sustaining
54 neural tissues, suggesting energetic conflict between these two demands (Winkler et al. 2004, McGuire
55 and Ratcliffe 2011). Migration is one of the most energetically challenging periods in a bird's life: Bar-
56 tailed Godwits (*Limosa lapponica*), for example, cover 11,000 km in a single non-stop flight (Gill et al.
57 2009). Such strenuous movements are often on the edge of avian physiological endurance and
58 necessitate a range of adaptations to make the journey possible (Hedenström 2010). For instance, we
59 know that body mass is often doubled during the pre-migratory fattening process to support the

60 energetic needs of the journey (Newton 2008), while almost all organs undergo significant size
61 reduction prior to migration to minimise the metabolic cost of transport (Piersma and Lindström 1997,
62 Battley et al. 2000). An extensive study on the morphological adaptations to migration in birds found
63 that heart size, the most calorie-hungry structure in the body, is relatively smaller in long-distance
64 migrants (Vágási et al. 2016), corroborating negative selection on energetically expensive organ sizes.
65 Given the energetic cost of flight, long-distance migration may compromise a bird's ability to support
66 the high metabolic cost of a large brain. Thus, the energetic trade-off hypothesis predicts directional
67 selection that favours smaller relative brain size with increasing migration distance.

68

69 In contrast, the behavioural flexibility hypothesis assumes a positive directional selection on relative
70 brain size in resident birds (Winkler et al. 2004) instead of negative selection in migrants. Resident bird
71 species often experience strong spatial and temporal fluctuations in their environments, and therefore
72 tend to rely more heavily on novel food sources, exploited through innovations and learning (Sol et al.
73 2005, Aplin et al. 2013). Classical examples of such behaviours are the ‘milk bottle’ innovation in Blue
74 Tits (*Cyanistes caeruleus*) (Aplin et al. 2013), or Great Tits (*Parus major*) predated on hibernating bats
75 (Estók et al. 2009). Such behaviours usually only happen under environmental conditions (e.g. harsh
76 winters) that limit normal food sources (Estók et al. 2009); this also highlights the importance of
77 innovation in seasonal and harsh environments. Indeed, innovation propensity and associated relative
78 brain size (Timmermans et al. 2000, Reader and Laland 2002), are both highest in resident species and
79 lowest in long distance migrants (Sol et al. 2005). Nonetheless, whether higher degrees of innovation in
80 resident species reflects necessity, or their capacity, has yet to be determined. To attempt to address this,
81 a reformulation of the behavioural flexibility hypothesis by inverting causalities was coined the
82 ‘migratory precursor hypothesis’ (Sol et al. 2005). The elevated cognitive capacity of large-brained
83 birds would enable them to be residents, while small-brained species are forced to migrate. Irrespective
84 of causality, higher cognitive needs, especially if innovative behaviour is socially transmitted (Aplin et
85 al. 2013), may represent one plausible explanation for the larger relative brain sizes of resident bird
86 species and might represent a coping mechanism to harsh or seasonal environments.

87

88 Exploring the relationship between relative brain size and the environmental harshness, or variability,
89 experienced by resident birds in different climatic zones, or latitudes, could provide a strong test of the

90 behavioural flexibility/migratory precursor hypothesis (Winkler et al. 2004). Studies investigating the
91 behavioural flexibility hypothesis to date are, however, scant and results are contradictory (Schuck-
92 Paim 2008). In neotropical parrots, climate variability was shown to be positively associated with
93 relative brain size (Schuck-Paim 2008), which provides some intraspecific support for the behavioral
94 flexibility hypothesis. Moreover, elevated winter harshness and the associated increased requirement
95 for food-caching is correlated with enlargement of brain regions responsible for spatial memory in
96 different Black-capped Chickadee (*Poecile atricapillus*) populations (Roth and Pravosudov 2009, Roth
97 et al. 2011). There is thus some evidence that the environmental harshness and fluctuation influence
98 brain evolution and functionality; however, which aspects of the environment are most important in this
99 respect, and in what settings do selective forces act, remain unanswered. By extending the geographical
100 and taxonomic coverage of previous studies, and by testing how different environments experienced by
101 species with similar migratory behaviours result in relative brain size differentiation could provide
102 potential answers to these questions.

103

104 In this study, I test separately the validity of the energetic trade-off and behavioural flexibility
105 hypotheses, and explore the nature of the negative correlation between relative brain size and migratory
106 behaviour in birds. First using data from the literature, I assess the generality of this negative
107 association on the basis of an extensive list of bird species ($n = 1,466$), across a very wide body size
108 (2.7 g - 44kg) and taxonomic range, encompassing ratites to passerines. Second, using migration
109 measured on a continuous scale (0 km – 13,063 km) and species with migration distance > 0 km (i.e.
110 excluding residents), I test the validity of the energetic trade-off hypothesis. This hypothesis will gain
111 support if there is a negative association between migration distance and relative brain size, and the
112 effect will be strongest among long-distance migratory birds. Third, using only resident species ($n =$
113 937), across a tropical-to-arctic distributional spectrum, I test the validity of the behavioural flexibility
114 hypothesis. In this final case, I use winter minimum temperature, seasonality of ambient temperature,
115 and wintering latitude to test which one of these factors best predicts the relative brain size of resident
116 birds. The behavioural flexibility hypothesis will be supported in cases where relative brain size
117 increases with latitude or seasonality, or decreases with increasing winter minimum temperature; note
118 that the latter ought to have the strongest effect when the nature of this association is defined by
119 environmental harshness. My study thus provides the first broad and fine scale mutual test for the

120 behavioural flexibility and energy trade-off hypotheses, to explore how these mechanisms shape the
121 evolution of avian brains.

122

123 **Materials and Methods**

124 **BRAIN AND BODY SIZE**

125 I extracted brain and body weight data from Iwaniuk and Nelson (2003), a primary dataset listing the
126 endocranial volumes of a wide range of birds. Endocranial volume is a highly reliable method to
127 measure brain size both across, and within, species (Iwaniuk and Nelson 2002). Brain mass was then
128 obtained by multiplying reported endocranial volumes by the density of fresh brain tissue, 1.036 g/mL
129 (Iwaniuk and Nelson 2003), and the dataset was then further modified by calculating a single mean for
130 species for which data was originally reported at the subspecies level (e.g. *Platycercus elegans elegans*
131 and *P. e. flaveolus*), or using two synonymous names (e.g. *Esacus magnirostris* and *E. neglectus*). In
132 these cases, species means were calculated as the weighted arithmetic mean of separate measurements
133 where weights were represented by the number of specimens measured in each case.

134

135 Given that larger-bodied species have larger brains, body mass needs to be controlled for when
136 comparing brain sizes across species (Lashley 1949). Body mass was therefore included in each of the
137 models presented here, as brain size relative to body size is a measure that reflects the surplus of neural
138 tissue versus the amount required for basic bodily functions (Lashley 1949), and is associated with a
139 range of cognitive traits across species (see above).

140

141 **MIGRATION DISTANCE**

142 Distribution maps (shape files) for each species were downloaded from
143 <http://www.birdlife.org/datazone/info/spcdownload> (BirdLife International and NatureServe 2014), and
144 the geometric centroid of the spatial polygon of breeding (breeding and resident) and wintering
145 (wintering and resident) ranges were calculated using the 'gCentroid' function in the R package 'rgeos'
146 (Bivan and Rundel 2013). Migration distance was calculated as the geographic distance between
147 breeding and wintering centroids using a custom function written in R (Vágási et al. 2016). 'Migratory
148 distance' thus denotes the average distance travelled by a given species during migration. Additionally,
149 I extracted the latitude of the non-breeding centroids, and calculated absolute values (thereafter, 'non-

150 breeding latitude').

151

152 **ENVIRONMENTAL HARSHNESS AND SEASONALITY**

153 I extracted ambient temperature data from the University of East Anglia Climate Research Unit
154 database (CRU, <http://www.cru.uea.ac.uk/>; version 3.10.01; Mitchell and Jones 2005), a global dataset
155 containing interpolated monthly average land temperatures (°C) from 1901 onwards in a grid of spatial
156 coordinates (0.5 × 0.5 degrees). I used the most recent temperature data ('cru_ts_3.23.2011.2014',
157 downloaded on 26 September 2015) comprising monthly temperature means from 2011 to 2014. First, I
158 averaged these four years to calculate mean monthly temperatures for each spatial grid cell. From the
159 resulting data file, I created a 12-layer shape file, where each layer contained a month's mean
160 temperature separately for each cell. Third, by intersecting temperature and species distribution shape
161 files, I calculated the monthly mean temperatures for each species, separately for their wintering and
162 breeding grounds. This resulted in 12 monthly means on the breeding ground, and 12 monthly means
163 on the wintering ground for each species. For the wintering ground, I extracted the lowest monthly
164 mean (thereafter, 'non-breeding minimum temperature') as a proxy of winter harshness. 'Seasonality'
165 was calculated as the difference between the lowest and highest monthly mean temperatures on the
166 breeding ground, and thus it reflects the extent of maximum thermal fluctuation during the course of a
167 year on the breeding ground for each species. Note that neither non-breeding minimum temperature nor
168 seasonality reflects the true environmental conditions experienced by species with migration distances
169 greater than 0 km. This is so, because long-distance migrants often do not experience the coldest
170 periods on the wintering grounds (e.g. July in South-America for White-rumped Sandpiper *Calidris*
171 *fuscicollis*), nor do they on the breeding grounds (e.g. January in North-America for the same species).
172 The latter is true for short-distance migrants too, due to their migratory tendencies under harsh
173 environmental conditions. Therefore, both non-breeding minimum temperature and seasonality were
174 only used in models based on species that have a migration distance of less than 1,000 km; the true
175 values of non-breeding minimum temperature and seasonality experienced by long distance migrants
176 could not be calculated due to lack of information on their temporal migratory patterns. In addition,
177 because non-breeding minimum temperature and seasonality could not be calculated for three fully
178 resident species with extremely restricted distributions (i.e., *Anas laysanensis*, *Porzana atra*, *Vini*
179 *stepheni*), sample size slightly varies between models with different explanatory variables.

180

181 **PHYLOGENY**

182 In order to implement the similarity of species due to common descent, I controlled for phylogenetic
183 relatedness in all analyses. To do this I downloaded 100 random trees from www.birdtree.org (Jetz et al.
184 2012) using the Hackett backbone tree (Hackett et al. 2008), and repeated every model with each of
185 these random trees to control for phylogenetic uncertainty (Rubolini et al. 2015).

186

187 **STATISTICAL ANALYSES**

188 I performed phylogenetic generalised least squares regressions (PGLS) using the ‘pgls’ function as
189 implemented in the R package ‘caper’ (Orme et al. 2013). Brain size was used as a dependent variable
190 in double predictor models, containing body mass and one of the following covariates: migration
191 distance, non-breeding minimum temperature, seasonality or non-breeding latitude. To test for the
192 energetic trade-off hypothesis, I built double predictor models containing migration distance and body
193 mass as explanatory variables on subsets of species over seven different migration distance intervals
194 (i.e. migration distance ≥ 0 km, >0 km, >500 km, $>1,000$ km, $>2,000$ km, >0 km & <500 km, >500 km
195 & $<1,000$ km). However, because the effect of migration distance might be confounded by the effect of
196 climate, given that these two often covary (i.e. species with longer migration distances experience
197 milder wintering climates), I repeated the above model using a subset of species with migration
198 distance $>2,000$ km, and with non-breeding range centroids within the tropics (23.4°N - 23.4°S). I
199 expect the strongest effect of migration distance on brain size in species with the longest migratory
200 trajectories if the energetic trade-off hypothesis is to be supported. Further, to test the behavioural
201 flexibility hypothesis, I built double predictor models containing body mass and non-breeding
202 minimum temperature, seasonality or non-breeding latitude, as explanatory variables on subsets of
203 species with five different migration distance intervals (i.e. migration distance = 0 km, <500 km,
204 $<1,000$ km, >0 km & <500 km, >500 km & $<1,000$ km). I expect the strongest effect of all three
205 variables in fully resident species, and that the strength of these associations will decrease with the
206 length of migration distance.

207

208 All the above analyses were repeated using passerines only, since these perching songbirds (order
209 Passeriformes) are less variable morphologically and trace their origins to a more recent common

210 ancestor than the non-passerines, but are more speciose and exhibit an impressive array of cognitive
211 abilities and migratory strategies (Sol et al. 2005). Moreover, models were repeated using non-
212 passerine bird orders with sufficient number of species and with considerable variance in the focal
213 explanatory variable. These orders were the *Anseriformes* and *Charadriiformes* for the energetic trade-
214 off hypothesis and *Piciformes*, *Strigiformes* and *Galliformes* for the behavioural flexibility hypothesis.
215 Taxonomic order was obtained using the 'tax_name' function as implemented in the R package 'taxize'
216 (Chamberlain et al. 2014), and each of the models described above was repeated with 100 random
217 phylogenetic trees; AICc scores extracted and AICc weights were calculated. AICc weights were then
218 used to calculate weighted mean t and p-values across the 100 models; distributions of both t and p
219 values of the focal explanatory variables in these model sets were plotted and are reported in
220 Supporting Information S1 (Table 1), and Supporting Information S2a and S2b (Table 2) for the entire
221 species and passerines respectively. Phylogenetic dependence was estimated using Pagel's λ , set to the
222 most appropriate value assessed by maximum likelihood in each model. Brain mass and body mass
223 were log-transformed prior to analyses, all other variables were used untransformed.

224

225 Migratory species often accumulate large amounts of fat to support their migratory flights (Newton
226 2008). Such body mass fluctuations might bias the results of brain size analyses in cases where
227 migratory species have larger body masses recorded in the dataset due to accumulated fuel reserves. In
228 these cases, relative brain size in longer distance migrants (with more fuel accumulated) would be
229 estimated erroneously as smaller. To rule out this confounding effect, I first tested whether mean body
230 mass used in the brain size models is correlated with migration distance (n = 1,466). Second, I obtained
231 data on minimum and maximum body mass from Dunning (2008) for 1,131 bird species present in the
232 brain dataset. Minimal and maximal body masses were obtained by averaging sexes, subspecies, and
233 populations if separate values were available, and on the basis of these data I tested whether the ratio
234 between minimum and mean body mass, as well as the ratio between maximum and mean body mass
235 covaries with migration distance. All three of these models were tested in a PGLS framework, using
236 100 phylogenetic trees. Results reported are weighted means (by AICc weights) of t- and P-values
237 calculated across the 100 models. Model averaging was performed in the same fashion as with brain
238 size models, and mean body mass and the two body mass ratios were all log-transformed prior the
239 analyses.

240

241 Graphical presentation of data was done using residual brain masses, calculated from a log-log standard
242 linear regression between brain mass and body mass. Fitted lines and associated standard errors were
243 obtained from the PGLS model between the residual brain mass and the focal predictor variable, and
244 standard errors were obtained using the 'predictSE.gls' function as implemented in R package
245 'AICcmodavg' (Mazerolle 2015). P values were not adjusted for multiple comparison, in order to
246 avoid inflation of the type II error probability (Rothman 1990, 2014). All statistical analyses and
247 graphical representations of results were carried out in R 3.2.0 (R Core Team 2015) and all data used in
248 the analyses are reported in Supporting Information S4.

249

250 **Results**

251 **DATA-SET COVERAGE**

252 Across the dataset (Fig. 1), migration distance varied from 0 km (n = 937 species) to 13,063 km in the
253 White-rumped Sandpiper (*Calidris fuscicollis*), while non-breeding latitude varied from 74.61° in the
254 Ivory Gull (*Pagophila eburnea*) to 0.01° in the Spot-winged Antbird (*Schistocichla leucostigma*). In
255 species with migration distance <1,000 km, non-breeding minimum temperature ranged from -29.05°C
256 in the Rock Ptarmigan (*Lagopus muta*) to 26.84° C in the Northern Screamer (*Chauna chavaria*), while
257 seasonality varied from 0.42°C in the Eyebrowed Jungle-flycatcher (*Rhinomyias gularis*) to 44.75°C in
258 the Asian Rosy Finch (*Leucosticte arctoa*).

259

260 **THE ENERGY TRADE-OFF HYPOTHESIS**

261 Brain size is strongly negatively correlated with migration distance across the entire migratory
262 spectrum (Table 1, Fig. 2A,D). This association disappears when fully resident species (migration
263 distance = 0 km) were excluded from analyses (Table 1). Indeed, when analyses were restricted to short
264 distance migrants (0 - 1,000km), the negative association between brain size and migration distance did
265 not emerge (Table 1, Fig. 2B,E) indicating that short distance migrants do not fit the relative brain size
266 – migration distance continuum when this is assessed using the entire migratory spectrum.
267 Nevertheless, the strength of the negative association between brain size and migratory distance
268 increased again, despite a reduction in sample size, after short-distance migrants were excluded (i.e.
269 subsets with migration distance from >500 km to >2,000 km, Table 1 and Fig. 2C,F). The negative

270 association between migration distance and brain size was also strong for the subset of species with
271 tropical wintering centroids and migration distances over 2,000 km. All results were highly consistent
272 when repeated just for passerines (Table 1, Fig. 2). Similar pattern was found in the case of
273 *Charadriiformes* and *Anseriformes*, but these associations did not reach significance (Supporting
274 Information S3, Table S1, Figure S1).

275

276 Mean body mass is negatively associated with migration distance (PGLS, $n = 1,466$, $t = -2.25$, $p =$
277 0.0035), indicating that longer distance migratory species have lower, not higher, average body masses
278 than species with shorter migratory distances. The ratio between minimum and mean body mass
279 decreased slightly with migration distance (PGLS, $n = 1,131$, $t = -2.54$, $p = 0.0120$), while the ratio
280 between maximum and mean body mass was strongly positively associated with migration distance
281 (PGLS, $n = 1,131$, $t = 3.42$, $p = 0.0008$).

282

283 **THE BEHAVIOURAL FLEXIBILITY HYPOTHESIS**

284

285 Non-breeding minimum temperature has a strong effect on brain size in both fully resident and short-
286 distance migratory species (Table 2, Fig. 3); the lower the non-breeding minimum temperature, the
287 larger the brain size (Table 2 and Fig. 3). Indeed, the effect of non-breeding minimum temperature was
288 comparable across different migratory intervals between 0 and 500 km, but not above 500 km (Table
289 2). In several species subsets, non-breeding minimum temperature is the only significant predictor of
290 relative brain size, while seasonality and non-breeding latitude have little predictive power. Where
291 significant, brain size increases with seasonality and increases with increasing non-breeding latitude
292 (Table 2); all results were highly consistent when repeated using just passerines (Table 2). Moreover,
293 results were highly consistent for the *Piciformes* and the *Strigiformes* bird orders, but none of the tested
294 environmental variables influenced brain size in the *Galliformes* bird order (Supporting Information
295 S3, Table S2, Figure S2).

296

297 **Discussion**

298 In this study, I show in the first place that whole brain size in birds is negatively correlated with
299 migration distance. This key result corroborates earlier studies (Sol et al. 2005, 2010, McGuire and

300 Ratcliffe 2011), but extends this negative correlation across much wider taxonomic and geographic
301 scales, and provides a basis for the generalisation of this association outside passerines. Secondly, my
302 study provides strong and clear support for the validity, and context, of the two alternative hypotheses
303 explaining the association between brain size and migration distance in birds, the energetic trade-off
304 and the behavioural flexibility hypotheses.

305

306 **ENERGETIC TRADE-OFF HYPOTHESIS**

307 Relative brain size in birds strongly decreases with increasing migration distance; this is true when
308 considering the entire migratory spectrum, or just long-distance migrants. First, results based on the
309 entire migratory spectrum corroborate earlier studies (Sol et al. 2005, 2010, McGuire and Ratcliffe
310 2011), and provide a basis for generalising the negative association between relative brain size and
311 migration distance across all birds. Note however, that the negative association between brain size and
312 migration distance was not significant in the two non-passerine bird orders tested, however both of
313 these show similar patterns. Second, results based just on long-distance migrants provide the
314 strongest support yet for the energetic trade-off hypothesis, indicating that it exists not just among
315 major migration distance subdivisions (e.g. residents, short-, and long-distance migrants), but also on a
316 fine scale within just long-distance migrants. One major drawback of earlier studies is that they
317 categorised species based on the length of their migratory trajectories; long-distance migrants were
318 handled within just one (Sol et al. 2005, McGuire and Ratcliffe 2011), or few categories (Sol et al.
319 2010). Here, I provide support for the energetic trade-off hypothesis by exploring fine-scale variations
320 of both migration distance and relative brain size within these categories, and results show that short-
321 distance migrants do not fit on the relative brain size – migration distance linear continuum. This
322 suggests that two different mechanisms control the evolution of the disparate relative brain sizes found
323 in migrants and residents, and that these mechanisms act on separate ends of the migratory spectrum. In
324 resident birds it is cognitive needs, while in migrants, energetic limitations appear to be important in
325 regulating brain size evolution. Results suggest that shorter-distance migrants are only partially affected
326 by both of these mechanisms.

327

328 Due to the correlative nature of this study, the negative association between migration distance and
329 relative brain size could potentially be confounded by several factors. First, the longer the migration

330 distance, the milder wintering conditions can get; therefore, the smaller brain size in long-distance
331 migrants could also be explained by the year-round milder environment these birds experience. Note
332 however that the negative association between brain size and migration distance is also apparent in
333 species with migration distances over 2,000 km, and with wintering range geometric centroids within
334 the tropics. This result suggests that the negative association between brain size and migration distance
335 is unlikely to be confounded by correlated climate effects, and that the nature of this association is
336 indeed an energetic trade-off. Second, given that migratory species often accumulate large fat reserves
337 to support their migratory flight, relative brain size might be underestimated if lean body mass is
338 overestimated in migrants. Such errors in the data could lead to a false identification of the energetic
339 trade-off hypothesis as true, given that larger fuel amounts are accumulated in longer distance migrants.
340 Note however, that mean body mass used in the analyses was actually negatively correlated with
341 migration distance in this dataset, indicating the migratory fuelling did not affect mean body mass
342 estimates used here. Additionally, for a subsample of species ($n = 1,131$) the ratio of minimum to mean
343 body mass decreased slightly with increasing migration distance. This weak association, compared to
344 the strong positive association between migration distance and the ratio of maximum to mean body
345 mass indicates that migratory fuelling is unlikely to largely distort mean body mass values used here
346 and is therefore unlikely to confound my results.

347
348 An earlier phylogenetic path analyses showed that the largest fraction (68%) of the correlation between
349 relative brain mass and migratory distance is a direct effect of migration on brain size (Sol et al. 2010).
350 Although these authors argued that brain size reduction in migrants could have originated from the
351 lowered importance of cognitive capacities in these birds (Sol et al. 2010), relative brain size in short-
352 distance migrants is not affected by migration distance. This result is important because cognitive needs
353 for resource exploitation in short-distance migrants might arguably be closer to those of long-distance
354 migrants than to those of residents simply because of their migratory tendencies in case of resource
355 shortages and their potentially decreased needs for innovation (e.g. irruptive or facultative migration,
356 Newton 2008). Therefore, it is unlikely that the brain size of long-distance migrants shrinks simply
357 because of a reduction in cognitive need, leaving the energetic trade-off hypothesis as a more plausible
358 explanation. This is especially the case given that the negative association between migration distance
359 in long-distance migratory species (over 2,000 km) and with tropical non-breeding ranges still holds

360 true, although cognitive needs within this group of birds could potentially be similar. Second, given that
361 migration is an extremely strenuous activity (Hedenström 2010), and the length of migration distance
362 was shown to negatively correlate with the energetically expensive heart size (Vágási et al. 2016), I
363 consider the pure energetic trade-off hypothesis to be the most likely explanation of brain size
364 reduction in long-distance migrants.

365

366 **THE BEHAVIOURAL FLEXIBILITY HYPOTHESIS**

367 Non-breeding minimum temperature is a strong predictor of relative brain size in fully resident (n =
368 934 species), and short-distance (up to 500 km, n = 142 species) migratory birds. In other words, the
369 colder the minimum monthly temperature on the wintering ground the larger the relative brain size of
370 birds. Additionally, relative brain size significantly increased with non-breeding latitude and
371 seasonality although these effects are weaker than the association with non-breeding minimum
372 temperature. Thus, my results strongly indicate that winter harshness is associated with larger brains
373 across the avian phylogeny. Given that non-breeding latitude and seasonality have weaker effects than
374 non-breeding minimum temperature on relative brain size, it is more likely that environmental severity
375 reflected by low ambient temperature, high snow cover, and/or reduced day length (Roth and
376 Pravosudov 2009), rather than the seasonal nature of the environment being the strongest selective
377 force on brain size evolution in resident birds. Indeed, the importance of climate severity in brain
378 evolution has previously been reported; food-caching Black-capped Chickadees from harsher
379 wintering ranges have better spatial memory, as well as larger hippocampi and higher neuronal density
380 in these brain regions responsible for this skill (Roth and Pravosudov 2009, Pravosudov and Clayton
381 2002, Roth et al. 2011). Enhanced spatial memory is thus a potential mechanism enabling birds to cope
382 with environmental harshness, especially in food-caching species. The hippocampus occupies just a
383 small part of total brain volume, however, and thus the results presented here must reflect additional
384 neural adaptations to environmental severity. To date we have very limited knowledge on how
385 environmental conditions, in particular which aspects of the environment and in which way does it
386 influence brain and cognitive evolution across species. The topic therefore deserves considerable future
387 scientific attention.

388

389 **FURTHER REMARKS**

390 Change in the size of different brain regions with migration distance is non-uniform (McGuire and
391 Ratcliffe 2011, Fuchs et al. 2014, Vincze et al. 2015), and reduction of whole brain size with increasing
392 migration distance is mostly accounted for by reduction in the size of the telencephalon (Vincze et al.
393 2015), the center of higher cognitive processes. In line with the latter results, Fuchs et al. (2015) found
394 that migratory lark sparrows (*Chondestes grammacus*) showed a clear trend toward having larger
395 nidopalliums (a central neural substrate of higher cognitive processes in birds) than residents of the
396 same species. Therefore, it is probable that the larger relative brain size of resident birds compared to
397 migrants is indeed associated with their larger telencephalon and better cognitive abilities that could
398 enhance their survival probability especially under harsh environmental conditions. It would be
399 insightful then to consider how environmental harshness in various resident birds influences the
400 evolution of different brain regions, on a cross-species scale. Such a follow-up study could provide
401 more precise insights into whether increase in the size of telencephalon (and regions thereof, e.g.
402 hippocampus) is specifically selected in species wintering under harsher environmental conditions.
403 Additionally, whether brain size enlargement preceded, or followed, the switch in migratory habit in
404 avian evolution is yet to be determined. Pravosudov et al. (2007) for instance examined three
405 subspecies of white-crowned sparrow (*Zonotrichia leucophrys*) and showed that it is more likely that
406 brain size enlargement took place after the switch from migratory to sedentary behaviour. Nonetheless,
407 further studies should examine the nature of these associations on a broader taxonomic scale.

408

409 Relative brain size variation is subtler in bats than in birds (McGuire and Ratcliffe 2011), and the
410 authors suggest that this discrepancy could originate from the shorter migration distances covered by
411 bats relative to birds. In addition, I suggest that besides the longer migration distances selecting for
412 smaller brains in both birds and mammals, harsh environments experienced by vigilant resident birds
413 (but not hibernating resident bats) will select for enlarged brains, further distancing relative brain
414 volume of resident from that of long-distance migratory birds.

415

416 Here I show that both environmental harshness and migration distance strongly affect brain size
417 evolution in birds. It's important to note however that these two factors appear to explain only a
418 fraction of the cross-species variance observed (see Fig 2,3). The extra variation is certainly explained
419 by other social, ecological, physiological or life-history factors not examined here that affect brain or

420 cognitive evolution across birds.

421

422 Importantly, comparative studies of full brain size have been subject to strong criticism in recent years
423 (Healy and Rowe 2007). The argument is that the brain is responsible for a wide range of functions,
424 therefore is not suitable to directly associate it with specific behaviours. However, a range of studies
425 indicate that relative brain size is a strong predictor of cognitive abilities, such as innovativity, learning,
426 invasion, tool use, memory, variability of habitats occupied (Schuck-Paim 2008, Sol 2009, Sol et al.
427 2007, 2010). Moreover, recent comparative evidence reveals that large brains in birds are a result of
428 disproportionately enlarged pallial areas known to play key roles in avian cognition (Sayol et al. 2016).
429 These studies suggest that whole brain size is indeed a useful tool of assessing general evolutionary
430 patterns of brain and cognitive evolution. The results obtained this way will naturally benefit from a
431 more specific research framework, where the change in specific brain regions is precisely assessed.

432

433 **CONCLUSIONS**

434 Here I demonstrate that increasing environmental harshness during the non-breeding period is
435 associated with larger relative brain sizes in both resident and short distance migrants and thus, in these
436 species, selection for behavioural flexibility must be an important driver of brain size evolution.
437 Nevertheless, because I also show that increasing migration distance is linked with decreased relative
438 brain size, the energetic trade-off hypothesis is also supported, especially in species with long
439 migratory flights. Taken together, this study illustrates that the selection for larger brain size by cold
440 wintering temperatures and the selection for smaller brain size by migratory flight both contribute to
441 the evolution of disparate relative brain sizes of migratory and resident bird species, and these two
442 mechanisms act on different ends of the migratory spectrum. Finally, it is important to note that I have
443 taken a correlative approach here, therefore the nature of causalities cannot be inferred from my results.
444 In other words, migratory habit or geographic distributions may select for larger or smaller brains, but
445 brain size evolution might as well precede switch in migratory strategy or define suitable distribution
446 ranges (Sol et al. 2005, Pravosudov et al. 2007).

447

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457

458 SUPPORTING INFORMATION

459 **Supporting Information S1:** These figures represent parameter distribution over 100 models with
460 different phylogenetic trees. Each row of the figure represents a row from Table 1. The first two
461 columns represent t- and P-values from models of the entire species pool, while the other two from
462 models of Passerines.

463 **Supporting Information S2:** These figures represent parameter distribution over 100 PGLS models
464 with different phylogenetic trees. Each row of the figure S2a represents a row from the first part of
465 Table 2 (i.e. entire species pool), while S2b from the second part of Table 2 (i.e. *Passerines*). 1st and 2nd
466 columns represent parameters from models containing non-breeding minimal temperature, 3rd and 4th
467 columns from models containing seasonality, 5th and 6th columns from models containing non-breeding
468 latitude.

469 **Supporting Information S3:** Models exploring the relationship between brain size and migration
470 distance (in two non-passerine bird-orders) as well as with non-breeding minimal temperature,
471 seasonality and non-breeding latitude (in three non-passerine bird orders). Results of models and
472 graphical presentation are both given.

473 **Supporting Information S4:** Data used in the analyses.

474

475 LITERATURE CITED

- 476 Aplin, L. M., B. C. Sheldon and J. Morand-Ferron. 2013. Milk bottles revisited: social learning and
477 individual variation in the blue tit, *Cyanistes caeruleus*. *Anim. Behav.* 85:1225-1232.
- 478 Battley, P. F., T. Piersma, M. W. Dietz, S. Tang, A. Dekinga and K. Hulsman. 2000. Empirical evidence
479 for differential organ reductions during trans-oceanic bird flight. *Proc. R. Soc. Lond. B*

480 267:191-195.

481 Bartoń, K. 2015. MuMIn: Multi-Model Inference. R package version 1.15.1. [http://CRAN.R-](http://CRAN.R-project.org/package=MuMIn)

482 [project.org/package=MuMIn](http://CRAN.R-project.org/package=MuMIn)

483 BirdLife International and NatureServe. 2014. Bird species distribution maps of the world. BirdLife

484 International, Cambridge, U.K.

485 Bivand, R. and C. Rundel. 2013. Rgeos: Interface to Geometry Engine - Open Source (GEOS). R

486 Package Version 0.3-2.

487 Chamberlain, S., E. Szocs, C. Boettiger, K. Ram, I. Bartomeus and J. Baumgartner. 2014. taxize:

488 Taxonomic information from around the web. R package version 0.3.0.

489 <https://github.com/ropensci/taxize>

490 Cristol, D. A., E. B. Reynolds, J. E. Leclerc, A. H. Donner, C. S. Farabaugh and C. W. S. Ziegenfus.

491 2003. Migratory dark-eyed juncos, *Junco hyemalis*, have better spatial memory and denser

492 hippocampal neurons than non-migratory conspecifics. *Anim. Behav.* 66:317–328.

493 Estók, P., S. Zsebők and B. M. Siemers. 2009. Great tits search for, capture, kill and eat hibernating

494 bats. *Biol. Lett.* 6:59–62.

495 Fuchs, R., H. Winkler, V. P. Bingman, J. D. Ross and G. Bernroider. 2014. Brain geometry and its

496 relation to migratory behavior in birds. *J. Adv. Neurosci. Res* 1:1-9.

497 Fuchs, R., V. P. Bingman, J. D. Ross and G. Bernroider. 2015. Brain contrasts between migratory and

498 nonmigratory North American lark sparrows (*Chondestes grammacus*). *NeuroReport* 26:1011-

499 1016.

500 Gill, R. E. Jr., T. L. Tibbitts, D. C. Douglas, C. M. Handel, D. M. Mulcahy, J. C. Gottschalek,

501 N. Warnock, N. J. McCaffery, P. F. Battley and T. Piersma. 2009. Extreme endurance flights by

502 landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proc. R. Soc.*

503 *Lond. B* 276:447–457.

504 Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W.

505 A. Cox, K. L. Han, J. Harshman et al. 2008. A phylogenomic study of birds reveals their

506 evolutionary history. *Science* 320:1763–1768.

507 Healy, S. D. and C. Rowe. 2007. A critique of comparative studies of brain size. *Proc. R. Soc. Lond. B*

508 274:453-464.

509 Hedenström, A. 2010. Extreme endurance migration: what is the limit to non-stop flight. *PLoS Biol*,

510 8:e1000362.

511 Isler, K. and C. van Schaik. 2006. Costs of encephalization: the energy trade-off hypothesis tested on
512 birds. *J. Hum. Evol.* 51:228-243.

513 Isler, K. and C. P. van Schaik. 2009. The expensive brain: a framework for explaining evolutionary
514 changes in brain size. *J. Hum. Evol.*, 57:392-400.

515 Iwaniuk, A. N., and J. E. Nelson. 2002. Can endocranial volume be used as an estimate of brain size in
516 birds? *Can. J. Zoolog.* 80:16-23.

517 Iwaniuk, A. N. and J. E. Nelson. 2003. Developmental differences are correlated with relative brain
518 size in birds: a comparative analysis. *Can. J. Zoolog.* 81:1913-1928.

519 Jetz, W., G. Thomas, J. Joy, K. Hartmann and A. Mooers. 2012. The global diversity of birds in space
520 and time. *Nature* 491:444–448.

521 Lashley, K. S. 1949. Persistent problems in the evolution of mind. *Q. Rev. Biol.* 24:28-42.

522 Lefebvre, L., S. M. Reader and D. Sol. 2004. Brains, innovations and evolution in birds and primates.
523 *Brain Behav. Evolut.* 63:233-246.

524 Lefebvre, L. and D. Sol. 2008. Brains, lifestyles and cognition: are there general trends? *Brain Behav.*
525 *Evolut.* 72:135-144.

526 Lefebvre, L. 2013. Brains, innovations, tools and cultural transmission in birds, non-human primates,
527 and fossil hominins. *Front. Hum. Neurosci.* 7:10-3389.

528 Mazerolle, M. J. 2015. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R
529 package version 2.0-3. <http://CRAN.R-project.org/package=AICcmodavg>.

530 McGuire, L. P. and J. M. Ratcliffe. 2011. Light enough to travel: migratory bats have smaller brains,
531 but not larger hippocampi, than sedentary species. *Biol. Lett.* 7:233-236.

532 Mitchell, T. D. and P. D. Jones. 2005. An improved method of constructing a database of monthly
533 climate observations and associated high-resolution grids. *Int. J. Climatol.*, 25:693-712.

534 Newton, I. 2008. *The ecology of bird migration*. Academic Press, London, U.K.

535 Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., and Pearse, W. 2014. caper:
536 Comparative Analyses of Phylogenetics and Evolution in R, R package version 0.5.2; 2013.
537 <http://CRAN.R-project.org/package=caper>

538 Piersma, T. and Å. Lindström. 1997. Rapid reversible changes in organ size as a component of adaptive
539 behaviour. *Trends Ecol. Evol.* 12:134-138.

540 Pravosudov, V. V. and N. S. Clayton. 2002. A test of the adaptive specialization hypothesis: population
541 differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile*
542 *atricapilla*). Behav. Neurosci. 116:515.

543 Pravosudov, V. V., K. Sanford and T. P. Hahn. 2007. On the evolution of brain size in relation to
544 migratory behaviour in birds. Anim. Behav. 73:535–539.

545 R Core Team. 2015. R: A Language and Environment for Statistical Computing. R Foundation for
546 Statistical Computing, Vienna, Austria.

547 Reader, S. M. and K. N. Laland. 2002. Social intelligence, innovation, and enhanced brain size in
548 primates. Proc. Natl. Acad. Sci. USA 99:4436–4441.

549 Roth, T. C. and V. V. Pravosudov. 2009. Hippocampal volumes and neuron numbers increase along a
550 gradient of environmental harshness: a large-scale comparison. Proc. R. Soc. Lond. B 276:401-
551 405.

552 Roth, T. C., L. D. LaDage and V. V. Pravosudov. 2011. Variation in hippocampal morphology along an
553 environmental gradient: controlling for the effects of day length. Proc. R. Soc. Lond. B
554 rspb20102585.

555 Rothman, K. J. 1990. No adjustments are needed for multiple comparisons. Epidemiology. 1:43–46.

556 Rothman, K. J. 2014 Six persistent research misconceptions. J Gen Int Med. 29:1060-1064.

557 Rubolini, D., A. Liker, L. Z. Garamszegi, A. P. Møller and N. Saino. 2015. Using the BirdTree. org
558 website to obtain robust phylogenies for avian comparative studies: A primer. Current Zool.
559 61:959-965.

560 Sayol, F., L. Lefebvre and D. Sol. 2016. Relative Brain Size and Its Relation with the Associative
561 Pallium in Birds. Brain Behav. Evolut. 87:69-77.

562 Schuck-Paim, C., W. J. Alonso and E. B. Ottoni. 2008. Cognition in an ever-changing world: Climatic
563 variability is associated with brain size in neotropical parrots. Brain Behav. Evolut. 71:200-
564 215.

565 Sol, D., N. Garcia, A. Iwaniuk, K. Davis, A. Meade, W. A. Boyle and T. Székely. 2010. Evolutionary
566 divergence in brain size between migratory and resident birds. PloS ONE 5:e9617.

567 Sol, D., L. Lefebvre and J. D. Rodríguez-Teijeiro. 2005. Brain size, innovative propensity and
568 migratory behaviour in temperate Palaearctic birds. Proc. R. Soc. Lond. B 272:1433–1441.

569 Sol, D., T. Székely, A. Liker, L. Lefebvre. 2007. Big-brained birds survive better in nature. Proc. R.

570 Soc. Lond. B 274:763-769.

571 Sol, D. 2009. Revisiting the cognitive buffer hypothesis for the evolution of large brains. Biol. Lett.
572 5:130-133.

573 Timmermans, S., L. Lefebvre, D. Boire and P. Basu. 2000. Relative size of the hyperstriatum ventrale is
574 the best predictor of feeding innovation rate in birds. Brain Behav. Evolut. 56:196-203.

575 Vágási, C. I., P. L. Pap, O. Vincze, G. Osváth, J. Erritzøe and A. P. Møller. 2016. Morphological
576 adaptations to migration in birds. Evol. Biol. 43: 48-59.

577 Vincze, O., I. C. Vágási, P. L. Pap, G. Osváth and A. P. Møller. 2015. Brain regions associated with
578 visual cues are important for bird migration. Biol. Lett. 11:20150678.

579 Winkler, H., B. Leisler and G. Bernroider. 2004. Ecological constraints on the evolution of avian brains.
580 J. Ornithol. 145:238-244.

581 **Table 1.** Models exploring the relationship between brain size and migration distance in birds with different migratory strategies. Each row
582 represents a separate model. All models include body mass as covariate (effect of body mass not shown). The first column provides the
583 criteria used to define the species pool for each model. t- and P-values shown here are weighted averages over 100 PGLS models with
584 different phylogenetic trees. The sign of t value indicates the direction of the association, while their value show the strength of association.
585 Results from analyses of the entire taxonomic range and restricted analyses of passerines are provided.
586

Migration distance restriction	Entire species pool				Passerine species			
	n	t-value	P-value	R²	n	t-value	P-value	R²
No restriction	1466	-5.37	<0.0001	0.89	610	-6.44	<0.0001	0.90
> 0 km	529	-3.11	0.0022	0.90	189	-4.22	<0.0001	0.92
> 500 km	387	-3.60	0.0004	0.90	143	-4.49	<0.0001	0.92
> 1,000 km	326	-2.74	0.0067	0.92	119	-3.82	0.0002	0.93
> 2,000 km	233	-3.60	0.0004	0.92	78	-3.42	0.0010	0.92
> 0 & < 500km	142	2.21	0.0319	0.92	46	2.47	0.0179	0.95
> 500 & < 1,000km	61	0.78	0.4415	0.87	24	0.48	0.6434	0.93
> 2,000 km & tropical wintering	146	-3.32	0.0012	0.92	58	-3.34	0.0015	0.90

587

588

589 **Table 2.** Models exploring the relationship between brain size and non-breeding minimum temperature, seasonality or non-breeding latitude
590 in birds with different migratory strategies. Each row represents a separate model. All models include body mass as covariate (effect of body
591 mass not shown). The first column provides the criteria used to define the species pool each model was based on. Where two sample sizes
592 are given, the first refers to the minimum temperate and the seasonality models, while the second to the non-breeding latitude model. t- and
593 P-values shown here are weighted averages over 100 PGLS models with different phylogenetic trees. The sign of t value indicates the
594 direction of the association, while their value show the strength of association. Results from analyses of the entire taxonomic range and
595 restricted analyses of passerines are provided.
596

Migration distance restriction	n	Non-breeding minimal temperature			Seasonality			Non-breeding latitude		
		t-value	P-value	R ²	t-value	P-value	R ²	t-value	P-value	R ²
Entire species pool										
0 km	934/937	-2.55	0.0134	0.89	0.53	0.6029	0.89	0.34	0.7274	0.89
< 500 km	1076/1079	-3.50	0.0007	0.89	1.38	0.1794	0.89	1.27	0.2153	0.89
< 1,000 km	1137/1140	-3.57	0.0005	0.89	1.24	0.2235	0.89	1.45	0.1572	0.89
0 > & < 500km	142	-4.14	0.0001	0.93	2.84	0.0060	0.93	3.84	0.0002	0.93
> 500 & < 1,000km	61	-1.83	0.0725	0.88	1.99	0.0524	0.88	2.17	0.0344	0.88
Passerines										
0 km	421	-2.77	0.0062	0.90	0.84	0.4021	0.90	1.79	0.0752	0.90
< 500 km	467	-3.70	0.0003	0.90	1.43	0.1556	0.90	2.42	0.0162	0.90
< 1,000 km	491	-3.27	0.0012	0.90	0.75	0.4598	0.89	2.10	0.0367	0.89
0 > & < 500km	46	-4.47	0.0001	0.97	3.36	0.0017	0.96	3.42	0.0014	0.96
> 500 & < 1,000km	24	-1.07	0.2974	0.94	0.47	0.6453	0.94	1.36	0.1871	0.94

598 **FIGURE LEGENDS**

599 **Figure 1.** Map illustrating geographic data coverage. Orange circles represent the geometric centroid of the breeding areas, green pluses
600 represent the geometric centroids of the wintering grounds of the studied species.

601

602 **Figure 2.** Association between migration distance and body-mass controlled residual brain weight in the entire species list (A), in species
603 with migration distance between 0 and 1,000 km (B), and in species with migration distance over 2,000 km (C). Figures D-E-F show the
604 same for passerines only. Note that figures are based on raw data points, therefore much of the variation can be accounted to phylogenetic
605 effects.

606

607 **Figure 3.** The association between non-breeding minimum temperature and body-mass controlled residual brain weight in fully resident
608 species (A), in species with migration distance between 0 and 500 km (B), and in species with migration distance between 500 and 1,000 km
609 (C). Figures D-E-F show the same for passerines only. Note that figures are based on raw data points, therefore much of the variation can be
610 accounted for by phylogenetic effects (e.g. green filled circles on figure 3A,B,C denote species from the *Galliformes* bird order).