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Big brains stabilize populations and facilitate colonization of variable habitats in birds

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1 Big brains stabilize populations and facilitate colonization of variable habitats in
2 birds

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12 13 **Summary paragraph**

14
15 The cognitive buffer hypothesis posits that environmental variability can be a major
16 driver of the evolution of cognition because an enhanced ability to produce flexible
17 behavioral responses facilitates coping with the unexpected. Although comparative
18 evidence supports different aspects of this hypothesis, a direct connection between
19 cognition and the ability to survive a variable and unpredictable environment has
20 yet to be demonstrated. Here, we use complementary demographic and
21 evolutionary analyses to show that among birds, the mechanistic premise of this
22 hypothesis is well supported but the implied direction of causality is not.
23 Specifically, we show that although population dynamics are more stable and less
24 affected by environmental variation in birds with larger relative brain sizes, the
25 evolution of larger brains often predated and facilitated the colonization of variable
26 habitats rather than the other way around. Our findings highlight the importance of
27 investigating the timeline of evolutionary events when interpreting patterns of
28 phylogenetic correlation.

29 30 **Introduction**

31
32 Enhanced encephalization, that is, a greater than expected brain mass for a given
33 body size¹, has evolved independently in numerous groups of animals despite its
34 stringent energetic demands and potential developmental costs²⁻⁴. The cognitive
35 buffer hypothesis posits that the repeated evolution of relatively large brains was
36 driven primarily by the adaptive benefits of being able to mount quick, flexible
37 behavioral responses to frequent or unexpected environmental change^{5,6}. In line
38 with this view, comparative studies have shown that more highly encephalized birds
39 have greater potential for behavioral innovation^{7,8}, lower mortality rates^{9,10}, and a
40 greater capacity to thrive in human-altered environments^{11,12}. In addition, highly
41 encephalized birds have been shown to preferentially occupy environments with
42 more variable climates¹³⁻¹⁵, where biotic and abiotic conditions change considerably
43 within and across years.

44
45 Although these findings are consistent with the cognitive buffer hypothesis,
46 questions remain regarding its validity as a general explanation for the evolution of

47 cognition. In particular, it is currently unclear whether the observed link between
48 survival and encephalization is specifically driven by an enhanced ability to cope
49 with environmental change or driven instead by other adaptive benefits. In addition,
50 a direction of causality in the relationship between encephalization and
51 environmental variation has not yet been established. Specifically, the cognitive
52 buffer hypothesis predicts that relatively large brains evolved in situ as a result of
53 selection for coping with environmental variation⁵. However, large brains could
54 have also evolved elsewhere and may have subsequently facilitated the colonization
55 of variable habitats, as suggested by recent reports that anthropogenic
56 introductions of highly encephalized vertebrates to novel habitats tend to have
57 higher success rates¹⁶⁻¹⁸. Here, we leverage the power of modern evolutionary
58 analyses, broad scale comparative data sets, and citizen science to clarify these
59 fundamental issues regarding the role of ecological variation in the evolution of
60 cognition. We begin by applying current state-of-the-art demographic analyses to
61 test directly the mechanistic assumption that enhanced encephalization improves
62 survival in variable habitats. We then apply models of correlated trait evolution to
63 formally assess the direction of causality in the observed correlation between the
64 occupancy of variable habitats and high encephalization in birds.

65 66 **Results**

67 68 *Estimating cognitive ability*

69 In line with prior large scale comparative studies on the evolution of cognition, we
70 use relative brain size as a proxy for cognitive ability¹. This metric acknowledges
71 that absolute brain size increases naturally in larger species, and estimates instead a
72 species' cognitive ability as the extent to which its brain is larger (or smaller) than
73 expected from its body size. The relative brain sizes used in our analyses were
74 computed as residuals from a phylogenetic generalized least squares regression of
75 ln brain on ln body size (slope = 0.59 ± 0.00 ; intercept = -2.48 ± 0.05 ; $\lambda = 0.87 \pm$
76 0.01), including the 2,062 bird species for which brain size is currently available
77 (see methods and supplemental data 2). While such proxy for cognition is clearly
78 indirect, we note that there is a growing body of experimental and correlative
79 evidence linking relative brain size with cognitive ability^{19,20}, and more specifically
80 with behavioral innovation^{21,22}.

81 82 *Does greater cognition improve survival in more variable environments?*

83 One way to directly evaluate whether enhanced cognition increases survival in more
84 variable environments is to explicitly test whether the interaction between
85 encephalization and environmental variability has a significant effect on population
86 dynamics. If behavioral flexibility facilitates coping with unexpected ecological
87 challenges, then we predict that population dynamics in highly encephalized species
88 should be buffered from environmental extremes and should therefore be less
89 affected by increased environmental variability as compared to those of small-
90 brained species.

91

92 We tested this prediction in a sample of North American land birds for which brain
93 size is known and time series data are sufficient to properly estimate year-to-year
94 variation in breeding population numbers²³ (N = 126 species, Supplementary Data
95 1). Demographic data for this analysis were obtained from the North American
96 Breeding Bird Survey²⁴, a yearly standardized assessment of breeding bird
97 abundances conducted since 1966 at thousands of locations across the continent.
98 Following the current community standards²⁵, we used hierarchical Bayesian
99 models to estimate regional population dynamics for each species in each North
100 American bird conservation region, hereafter BCR (Fig. 1a). BCRs are ecologically
101 distinct regions²⁶ and are widely regarded as suitable biogeographic units for the
102 quantification of population dynamics²³. The hierarchical models implemented here
103 estimate yearly fluctuations in abundance while accounting for long-term
104 population trends, route-to-route variation in abundance, and imperfect detection
105 by observers (Fig. 1; see methods). By explicitly separating the sources of error in
106 reported bird counts, these models allow us to estimate the extent to which year-to-
107 year fluctuations in true population size are a product of ecologically relevant
108 processes such as the mortality induced by environmental extremes (also known as
109 “process error” or σ_{γ} ; Fig. 1). Species-specific abundance-weighted averages of the
110 process error, $\bar{\sigma}_{\gamma}$ (see methods) were subsequently used to test the hypothesis that
111 population stability is less affected by environmental variability in larger-brained
112 species. To better align our metrics with the narrative of this hypothesis, the
113 dependent variable in these downstream analyses was the negative of $\bar{\sigma}_{\gamma}$, hereafter
114 ‘population stability’, such that higher stability scores reflect cases with less
115 pronounced year-to-year fluctuation in population size.

116
117 We used phylogenetic generalized least squares (PGLS) regression models
118 estimated across a sample of 1,000 tree topologies from Jetz et al.²⁷ to investigate
119 the potential effects of environmental variability and encephalization on population
120 stability. Environmental predictors for these models included the mean, within-year
121 variance, and predictability of temperature, precipitation, and net primary
122 productivity (see methods). Predictability was estimated through Colwell’s P, an
123 index that captures variation among years in the onset, intensity, and duration of
124 periodic phenomena²⁸. Given the strong spatial covariance that is typically observed
125 among environmental parameters²⁹, all environmental variables were first
126 extracted globally at a spatial resolution of 0.5 by 0.5 degrees and subsequently
127 reduced to composite variables at the same resolution using principal components
128 analysis, PCA (Table 1, Supplementary Fig. 1a and b, and methods). Because
129 environmental correlations are often region specific³⁰, the PCA for this regional
130 analysis included only map cells located within our North American study region.
131 The first principal component recovered from this analysis showed a clear
132 latitudinal trend, where lower scores occurred primarily in northern, more seasonal
133 climates with colder and less predictable temperatures and high scores occurred in
134 Southwestern sites with hotter temperatures and more variable, unpredictable
135 precipitation patterns (Supplementary Fig. 1a). The second component of the North
136 American environmental PCA captured differences in mean precipitation as well as
137 in mean, variance, and predictability of net primary productivity. In this case, higher

138 scores indicated wetter environments with higher, but more seasonal and
139 unpredictable productivity including those found along the pacific coast of the
140 northern US and Canada, boreal forests, and much of the eastern US. Low scores for
141 PC2 were found in southwestern deserts and in the far North (Supplementary Fig.
142 1b).

143
144 When characterizing the typical habitats of each species in our sample, we
145 considered both spatial distribution and geographic variation in abundance. We first
146 calculated mean environmental components for every North American BCR
147 ($\overline{PC1}_{BCRi}$ and $\overline{PC2}_{BCRi}$). Then, we estimated species-specific habitat values, hereafter
148 H1 and H2, by computing the weighted averages of $\overline{PC1}_{BCR}$ and $\overline{PC2}_{BCR}$, where
149 weights were proportional to the relative abundance of the species in each BCR.
150 Correlation between H1 and H2 was high ($r = -0.56$; Supplementary Fig. 1c), so we
151 excluded the latter from our list of predictors to prevent possible multicollinearity
152 and unnecessary variance inflation. The decision to keep H1 rather than H2 was
153 based on the fact that H1 most directly captures the measures of variability that are
154 relevant for testing the mechanism behind the cognitive buffer hypothesis. We note
155 that both high and low values of H1 reflect increasingly variable and unpredictable
156 conditions. Specifically, low H1 scores indicate variable temperatures, whereas high
157 scores indicate variable precipitation. Thus, to explore the general effects of
158 environmental variability on population dynamics, we included H1 as a quadratic
159 term ($H1^2$) in our models of population stability. Because H1 is centered at zero, this
160 quadratic term captures the potential effects of both variable temperatures and
161 variable precipitation, and is therefore labeled 'environmental variability' hereafter.

162
163 We also took into account the possibility that population stability is influenced by a
164 variety of life history and ecological traits. First, we accounted for potential
165 relationships between relative population variability and population size³¹ by
166 including log-transformed mean abundance as a covariate in our models.
167 Additionally, we considered that environmental variability could affect population
168 dynamics through interactions with traits other than brain size. For example, we
169 considered that lifespan could be a predictor of populations stability because longer
170 lived species tend to exhibit higher adult survival³², and we included an interaction
171 with environmental variability ($H1^2$) because highly unpredictable conditions may
172 prevent individuals from realizing their maximum lifespan potential. Similarly, we
173 considered the fact that species with higher annual reproductive output may
174 experience more intense year-to-year population oscillations³³ and that this effect
175 could potentially be amplified in more variable habitats. Additionally, we explored
176 the possibility that variable conditions have weaker effects on the population
177 dynamics of large-bodied species because those species tend to be more resilient to
178 periods of resource scarcity³⁴. The same may be true for cooperative breeders –
179 which appear to be able to buffer the effects of harsh years through helping at the
180 nest³⁵, for species with generalist habits –which are typically able to exploit a wider
181 variety of environmental conditions³⁶, and for migrants –which typically avoid the
182 harshest conditions of their breeding grounds by temporarily leaving the area²⁹.
183 Further details on how these traits were defined and quantified can be found in the

184 methods. All of our data on population stability, brain size, ecology, and life history
185 are available in supplemental data 1.

186

187 Our demographic analysis revealed that a number of ecological traits are
188 significantly associated with population variability (adjusted R^2 for PGLS model =
189 0.22; Table 2). We found that while populations of resident species are less stable in
190 increasingly variable environments, migratory species maintain relatively stable
191 populations across all types of environments ($\bar{p} \ll 0.001$; Fig. 2a). Similarly, long-
192 lived species were found to exhibit more stable dynamics than short-lived ones only
193 in the most mild, predictable environments ($\bar{p} \ll 0.001$; Fig. 2b), indicating that the
194 potential benefits of long life spans may diminish when conditions are uncertain.
195 Consistent with the idea that cognitive ability improves survival in variable
196 environments, we found a significant interaction between encephalization and $H1^2$.
197 Specifically, while species with high encephalization were found to maintain
198 relatively stable populations in both stable and variable environments, those with
199 low encephalization showed a significant decline in population stability as
200 environmental variability increased ($\bar{p} \ll 0.001$; Fig. 2c). Our findings are
201 qualitatively similar when phylogenetic relationships are estimated from a
202 consensus tree rather than across a sample of tree topologies (Supplementary Table
203 1).

204

205 Although these initial results support the basic mechanistic premise of the cognitive
206 buffer hypothesis, the hierarchical models described above do not account for the
207 fact that variation in population size can be driven not only by exogenous
208 (environmental) factors, but also by internal, or density dependent factors. In the
209 context of hierarchical modeling, density dependent processes can be investigated
210 by modeling an explicit demographic process that assumes that true population
211 sizes oscillate around a demographic equilibrium value that does not change over
212 time³⁷ (e.g., the Gompertz function³⁸). This assumption is nevertheless clearly
213 violated whenever populations undergo long-term changes in mean abundance, as
214 is the case in many North American land birds³⁹ and nearly 80% of the species in
215 our dataset. Because models with density dependence are known to perform poorly
216 in such species⁴⁰, we explored the effects of density dependence exclusively on the
217 subset of species that did not show any evidence of long-term changes in mean
218 abundance in our initial set of demographic analyses. Given the relatively small
219 number of species in this category ($n = 27$), these confirmatory analyses could not
220 meaningfully explore the entire set of initial predictors and were therefore focused
221 on evaluating only the potential effects of relative brain size, $H1^2$, and their
222 interaction. These more narrowly defined analyses indicate that accounting for
223 density dependence does not change our main finding. That is, the interaction
224 between relative brain size and environmental variability is significant in PGLS
225 models based on the consensus tree (relative brain size* $H1^2$: $\beta = 0.63$, $p = 0.04$;
226 relative brain size: $\beta = -0.05$, $p = 0.84$; $H1^2$: $\beta = -0.35$, $p = 0.01$), and marginally
227 significant across the entire sample of 1,000 tree topologies (relative brain size* $H1^2$:
228 $\bar{\beta} = 0.61$, $\bar{p} = 0.06$, $f = 0.41$; relative brain size: $\bar{\beta} = -0.04$, $\bar{p} = 0.88$, $f = 0$; $H1^2$: $\bar{\beta} = -$
229 0.32 , $\bar{p} = 0.02$, $f = 1.00$). The marginal significance observed in the latter case

230 highlights the greater effect of phylogenetic uncertainty and the generally low
231 statistical power of comparative tests that are based only on a small number of
232 species.

233

234 *Did larger brains evolve in more variable environments?*

235 Our demographic analyses lend support to the underlying mechanistic premise of
236 the cognitive buffer hypothesis, which is that higher encephalization can improve
237 survival, specifically when environmental conditions are increasingly unstable.
238 However, in order to evaluate the extent to which this mechanism provides a
239 general explanation for the evolution of cognition in birds, it is critical to explore the
240 direction of causality in the correlation between an enhanced potential for cognition
241 and the occupancy of variable environments. A clear understanding of the sequence
242 of evolutionary events is particularly necessary in this context because the adaptive
243 benefits invoked by the cognitive buffer hypothesis may just as well promote the
244 evolution of cognition in variable habitats, or facilitate instead the secondary
245 colonization of variable habitats by already highly encephalized species⁴¹.

246

247 We evaluated the support for these two non-mutually exclusive evolutionary
248 scenarios by using reversible-jump MCMC to estimate models of correlated trait
249 evolution⁴² fitted to an exhaustive global sample of non-migratory birds for which
250 brain size is known (N = 1,288 species; Supplemental Data 2). These models allow
251 inference into potential evolutionary timelines by assessing the likelihood that rates
252 of evolutionary transitions between states of a binary trait (e.g. moderate to large
253 encephalization) are dependent on the state of a second binary trait (e.g. stable vs.
254 variable environmental habitats). In the context of the cognitive buffer hypothesis,
255 these models allow us to test whether the transition from small to large brains is
256 indeed more likely in variable than in stable environments (i.e., whether variable
257 environments tend to predate large brains). Similarly, these models allow us to
258 evaluate the likelihood of alternative, yet non-mutually exclusive timelines such as
259 the ‘colonization advantage’ scenario, which predicts that the transition from stable
260 to variable environments should be more likely in large- than in small-brained
261 species.

262

263 As in our demographic analysis, environmental variables were first extracted for the
264 relevant study region (here, the entire globe) and subsequently reduced to
265 composite variables through PCA (Supplementary Table 2). The first component of
266 this global PCA, hereafter ‘temperature variability’, captured a gradient of increasing
267 exposure to colder, more seasonally variable and less predictable temperatures
268 (Supplementary Fig. 1d). The second component, hereafter ‘xeric variability’,
269 captured a gradient of increasing exposure to drier and less productive
270 environments with more unpredictable precipitation (Supplementary Fig. 1e).
271 Species-specific habitats were characterized in this case by computing the mean
272 values of local temperature and xeric variability across entire breeding distributions
273 (see Methods).

274

275 Because transition rate analyses require discrete trait states, we explored a
276 reasonable range of thresholds for classifying species as having either small or large
277 encephalization, and as being exposed to highly variable or fairly stable
278 environments (30th, 50th, 75th and 90th percentile, see methods). Encephalization
279 categorizations were based on whether a species' relative brain size was above or
280 below the predefined threshold. Similarly, exposure to environmental variability
281 was considered high for a given species if either or both environmental principal
282 component scores belonged in a percentile above the predefined threshold.
283 Considering information from both principal components when characterizing
284 exposure to environmental variability allowed us to maintain consistency with our
285 demographic analyses (see Table 1), and to explore the general effects of
286 environmental variability rather than the specific effects of temperature or
287 precipitation variation.

288
289 Our models of correlated trait evolution do not support the main prediction of the
290 cognitive buffer hypothesis under any combination of thresholds. Specifically, the
291 evolution of larger relative brain sizes was generally found to be equally likely for
292 species occurring in stable environments and in harsher, more variable ones (i.e.,
293 there was no support for a difference in transition rate from moderate to large
294 encephalization between environment types; Bayes Factor (BF) < 3; Fig. 3d and f;
295 Supplementary Table 3). Furthermore, under certain classification criteria, we even
296 find evidence that advanced encephalization could be more likely to evolve in stable
297 than in highly variable habitats (e.g., highly variable environments: >50th percentile;
298 large encephalization: >50th percentile; BF = 3.15; Fig. 3a and c; Supplementary
299 Table 3). Collectively, these results indicate that while environmental variability can
300 theoretically select for enhanced cognition, it is in fact unlikely to have driven many
301 of the major transitions towards large brains in birds.

302
303 In stark contrast, we found that the evidence of an improved colonization ability of
304 variable habitats in highly encephalized avian lineages is both general and strong
305 (Fig. 3 b, c, e, and f; Supplementary Table 3). Such colonization advantage appears to
306 be specifically linked to an improved ability to deal with environmental variability
307 because we did not find support for a difference in transition rate from variable to
308 stable habitats between species with small and large encephalization values
309 (Supplementary Table 3). Additionally, our results indicate that even moderate
310 enhancements in cognitive ability and/or moderate increases in environmental
311 variability can help accrue such advantages: when thresholds for classification are
312 too conservative (e.g., variable environments: >90th percentile; large
313 encephalization: >75th percentile), differences in transition rates from stable to
314 variable environments are no longer detectable between very-large and
315 moderately-large brained species.

316 317 **Discussion**

318
319 Our demographic analysis broadly supports the notion that enhanced cognition can
320 lead to more stable population dynamics. Furthermore, the significant interaction

321 between H1² and encephalization is consistent with the idea that these benefits can
322 be generally accrued under different types of environmental variability and
323 unpredictability (see Table 1). We therefore conclude that there is general support
324 for the proposed mechanism underlying the cognitive buffer hypothesis, which is
325 that bigger than expected brains improve survival when environmental change is
326 frequent and unexpected.

327

328 Despite this finding, our transition rate analyses strongly indicate that the general
329 timeline of evolutionary events suggested by the cognitive buffer hypothesis is not
330 broadly supported across the avian phylogeny. Specifically, our results
331 unambiguously indicate that evolutionary transitions towards occupancy of more
332 variable habitats did not generally precede the evolution of enhanced
333 encephalization in birds. Ancestral state reconstructions facilitate the visualization
334 of this result (Fig. 4): several of the most highly encephalized clades in the bird
335 phylogeny (e.g., parrots, bowerbirds, and hornbills) evolved big brains without any
336 apparent exposure to particularly harsh or variable habitats throughout their
337 evolutionary history (Fig. 4 b, c, and e). Furthermore, even in clades that currently
338 occupy variable habitats (e.g., corvids or woodpeckers), it is unclear that exposure
339 to relatively high ecological variability preceded the evolution of larger brains (Fig.
340 4 d and f). Why then do we see today a correlation between variable habitats and
341 encephalization? Our analyses suggest that this correlation results from either the
342 preferential colonization of variable and unpredictable habitats by highly
343 encephalized species, or the preferential persistence of these highly encephalized
344 species in habitats that underwent major environmental change and became more
345 variable. One possible reason for this pattern is that highly encephalized birds have
346 lower risk of extirpation during the early stages of colonization (i.e., when
347 abundances are low⁴³), because of their enhanced ability to withstand
348 environmental change. Similar links between cognition and range expansion have
349 been made in studies documenting the success of highly encephalized species in
350 colonizing novel habitats^{16,17,41} and are the basis of our current understanding of the
351 process of human expansion out of Africa^{8,44}.

352

353 Overall, our results suggest that even though environmental variability can be a
354 viable agent of selection in the evolution of cognition (as also concluded by ^{14,45}),
355 this particular mechanism is unlikely to have driven many of the most striking cases
356 of encephalization among birds. It is nevertheless possible that other types of
357 ecological variability not included in this study can explain such transitions. For
358 example, although many parrots and hornbills tend to occupy habitats with fairly
359 stable climates, these species must typically cope with high levels of variation in the
360 location and timing of fruiting trees (a similar situation is likely to occur in other
361 species with complex feeding ecologies⁴⁵). While we acknowledge that a broad
362 interpretation of “variability” can increase the scope and generality of the cognitive
363 buffer hypothesis⁵, we note that overgeneralization may lead to the inadvertent
364 mischaracterization of very different types of selection (e.g., problem solving, long-
365 term memory, or spatial awareness), as different but equivalent forms of a single
366 process. A perhaps more fruitful approach would therefore be to explore the

367 possibility that there is no single primary driver in the evolution of relatively large
368 brains, and that this process is instead driven by the combined effects of both the
369 constraints²⁻⁴ and the various potential adaptive benefits of increased processing
370 capacity, including the ability to respond more quickly to novel challenges^{46,47},
371 navigate more complex social interactions^{48,49}, process more intricate sensory
372 information⁵⁰, and cope with greater spatial and/or temporal variability^{15,22}. As data
373 on these different processes become more readily available, we are confident that
374 future comparative studies will be able to disentangle the relative extent to which
375 these different forces have shaped the evolution of cognition at different taxonomic
376 scales. In the mean time, we hope that the realization that variation brain size was
377 more likely to shape the distribution of bird species across the globe rather than the
378 other way around can help inform more immediate research agendas.

379 **Methods**

380

381 *Quantification of relative brain size*

382 Our estimates of relative brain size were based on body size data from Myhrvold et
383 al. 2015⁵¹ and brain size data either from published accounts (N = 1,949 species;
384 cited in Supplementary Data 2) or measured directly by ANI (N = 113 species). Our
385 total brain data set includes several species that are not used in either our
386 demographic or correlated trait evolution analyses. Specifically, pelagic species
387 (orders Sphenisciformes, Suliformes, Procellariiformes, and Phaethontiformes;
388 families Pelecanidae, Laridae, Stercorariidae, and Alcidae) were initially included
389 when computing encephalization values but were subsequently excluded from
390 downstream analyses because land surface temperature and precipitation values
391 are unlikely to be indicative of the actual conditions experienced by species that
392 spend most of their time at sea. All brain size measurements collected by ANI were
393 obtained following the procedures outlined in Iwaniuk and Nelson (2002,
394 2003)^{3,52}. Briefly, the foraminae of the cranial nerves are sealed with masking tape
395 and lead shot is poured into the foramen magnum. To prevent the formation of
396 lacunae, the skull is lightly tapped throughout this procedure. Once the shot has
397 risen to the foramen magnum, the contents are decanted into modified syringes or
398 graduated cylinders to determine volume. This method is highly repeatable and
399 provides an accurate estimate of brain size in birds^{52,53}. Brain sizes that were
400 originally reported as volumes in the literature were converted to mass by
401 multiplying mL by the average density of fresh brain tissue (1.036g/mL)⁵².

402

403 To account for phylogenetic uncertainty, the log-log regression of brain size on body
404 size was independently run on 1,000 randomly selected tree topologies with the
405 Hackett backbone in Jetz et al.²⁷ (www.birdtree.org; downloaded July 14th, 2016).
406 The encephalization values used in all of our downstream analyses were computed
407 as the median residuals for each species across these 1,000 models.

408

409 *Characterization of environmental variability*

410 The environmental variables we consider here include the mean, within-year
411 variance, and predictability of temperature, precipitation, and net primary
412 productivity. Monthly raster maps of temperature and precipitation values were
413 obtained for years 1900 to 2005 from ecoClimate.org (provided at 1° resolution,
414 resampled to 0.5° resolution; downloaded July 25th, 2016)⁵⁴. Monthly net primary
415 productivity data for years 2000 to 2016 were obtained from the MODIS dataset
416 downloaded from NASA Earth Observations (provided at 0.5° resolution;
417 <http://neo.sci.gsfc.nasa.gov>, accessed March 18, 2016). Predictability was measured
418 as Colwell's P²⁸, an information-theory-based index that captures variation in the
419 onset, intensity, and duration of periodic phenomena and ranges from 0 (completely
420 unpredictable) to 1 (completely predictable).

421

422 Because environmental variables tend to be strongly correlated²⁹, we reduced the
423 original set of environmental predictors (transformed when required⁵⁵, centered,
424 and scaled) through principal component analysis, PCA. Separate analyses were

425 conducted to reduce the dimensionality of environmental data in the demographic
426 and correlated trait evolution sections to account for the fact that environmental
427 correlations are often region-specific³⁰. In the demographic analyses, the
428 environmental PCA was based only on North American data, including all cell values
429 north of the US-Mexico border (i.e., only the geographic region where breeding bird
430 survey data is available). In the correlated trait evolution analyses, the
431 environmental PCA included all global terrestrial habitats, excluding Antarctica.
432 Both environmental PCAs recovered similar components (see main text, Table 1,
433 and Supplementary Table 2 for details). In the demographic analysis, the average
434 score for each principal component was initially computed for every bird
435 conservation region and these regional averages were subsequently used to
436 characterize species-typical habitats. Specifically, variables H1 and H2 were
437 computed as weighted averages of the corresponding environmental components
438 (PC1 and PC2), where weights were determined by the species' relative abundance
439 in each conservation region. Species-typical environmental values for the global
440 analysis of correlated trait evolution were estimated directly by averaging all local
441 (0.5° by 0.5° cell) PCA scores across the species' entire breeding distribution.
442

443 *Bird population data*

444 Abundance data for our population dynamics analyses was collected between 1966
445 and 2014 by the North American Breeding Bird Survey (BBS; available through
446 www.pwrc.usgs.gov/bbs/, downloaded August 28th, 2015)²⁴. The BBS is
447 coordinated by the US Geological Survey (USGS) and the Canadian Wildlife Service
448 and conducted annually by trained volunteers during the height of the breeding
449 season. Participants travel along 24.5-mile roadside routes, conducting 3-minute
450 point count surveys at 0.5-mile intervals – recording every bird seen or heard
451 within a 0.25-mile radius. Each BBS survey route was assigned to a single Bird
452 Conservation Region (BCR) based on route starting coordinates²³. BCR maps were
453 provided by the USGS Patuxent Wildlife Research Center (www.pwrc.usgs.gov,
454 downloaded September 15, 2015). Only surveys fulfilling BBS quality criteria (i.e.
455 $\text{runtype} = 1$) were included in our analyses.
456

457 *Quantification of population dynamics*

458 We characterized the temporal dynamics of bird populations within BCRs across
459 North America using hierarchical Bayesian models following Smith et. al, 2014²⁵.
460 The log of abundance, $x_{j,i,t}$, for a given species at survey route j within BCR i in year t
461 is modeled as:

$$462 \log(x) = S_i + \beta_i * t + \gamma_{i,t} + \omega_{ij} + \eta I(j,t) + \varepsilon_{ij,t}$$

463

464 where S_i is the average abundance within BCR i , β_i is the temporal trend in
465 abundance within BCR i , and η is the first-year observer effect where $I(j,t)$ is 1 if the
466 survey at year t is an observer's first record at route j and 0 otherwise. Year effects, $\gamma_{i,t}$,
467 and route-observer effects, ω_{ij} , are modeled as BCR specific random effects, whereas
468 $\varepsilon_{ij,t}$, was modeled as a general random effect of count overdispersion. Given the
469 potential for differences in observer ability, a separate value of ω is given to each

470 unique route-observer combination. To account for imperfect detection during
471 surveys, the observed count on route j within BCR i during year t is assumed to have
472 a Poisson distribution with mean $x_{j,i,t}$. Abundances are allowed to vary among survey
473 routes within a BCR, but all routes are assumed to follow the same relative temporal
474 trend (β_i) and to undergo the same yearly fluctuations around this trend ($\gamma_{i,t}$). The
475 variance of route-observer effects within a BCR, $\sigma^2_{\omega_i}$ is drawn from a global
476 hyperdistribution. To conform with the assumption of normality of residuals in
477 general linear models, we use the negative of the standard deviation in annual
478 fluctuations ($-1*\text{sqrt}(\sigma^2_{\gamma_i})$) as our dependent variable in subsequent analyses of
479 population stability. The sign inversion is simply done to facilitate interpretation of
480 our results, such that higher values reflect more stable populations.

481
482 Because hierarchical models tend to underestimate the magnitude of annual
483 fluctuations when the number of missing survey years is high⁵⁶, we estimated
484 trends for a period when survey data is relatively consistent, namely from 1985
485 onwards. In addition, we improved data quality by including only route-observer
486 combinations with 10 or more years of survey data and estimating only parameters
487 for BCRs with at least 20 years of survey data and a minimum of 14 survey routes³⁹.
488 Model parameters were estimated with MCMC analysis using package ‘rjags’⁵⁷. Four
489 independent chains were run for each model, each of which included a burnin of
490 25,000 steps, an additional chain length of 25,000 steps and a thinning interval of
491 10. Priors for S_i , β_i , and η were normal distributions with mean of 0 and variance of
492 10^6 . Prior distributions for variances were inverse gamma distributions with scale
493 and shape equal to 0.001. Our assessment of chain convergence was done through
494 the ‘coda’ package in R⁵⁸ and included both a visual inspection of the traces of
495 posterior estimates and an estimation of potential scale reduction factors (PSRF) via
496 Gelman and Rubin’s convergence diagnostic⁵⁹. Only estimates obtained from BCRs
497 in which PSRF values were under 1.1 for all parameters (i.e., chains with proper
498 convergence) were included in our subsequent analyses of population stability. We
499 considered positive support for temporal trends when the 95% credible interval of
500 β_i did not include zero.

501
502 Hierarchical models with density dependence were also fitted to all species that did
503 not exhibit evidence of linear trends in our initial analysis ($n = 27$). Specifically, we
504 re-estimated population stability for these species using a discrete time, stochastic
505 Gompertz model following Dennis *et. al*, 2006³⁸. These models estimate density
506 dependent population change at the route level while allowing random
507 environmentally driven fluctuations and accounting for observer error in reported
508 abundances. The log of abundance at time t , $\log(x_t)$, is modeled here as a function of
509 $\log(x_{t-1})$:

$$\log(x_t) = a + b*\log(x_{t-1}) + E_t$$

512
513 where a is the intrinsic rate of increase and b is the strength of density dependence.
514 Values of b were allowed to range from -1 (strong) to 1 (no density dependence)³⁷.

515 Relative annual fluctuations, E_t , have a normal distribution with mean zero and
516 variance σ^2_E . Similarly, the log of observed counts in year t is assumed to have a
517 distribution with mean of $\log(x_t)$ and a variance of τ^2 . To conform with the
518 assumption of normality of residuals in general linear models, we used the negative
519 log of the estimated year-to-year variance (i.e., $-1 \cdot \log(\sigma^2_E)$), as our dependent
520 variable in subsequent analyses of population stability. As above, the sign inversion
521 here is simply done to facilitate interpretation of our results, such that higher values
522 reflect more stable populations. Data quality checks for hierarchical models with
523 density dependence, included estimating only models for routes with at least 20
524 years of survey data from 1985 onwards and no more than three consecutive years
525 of missing data. Parameters were estimated using MCMC analysis with four
526 independent chains, each ran with a burnin period of 100,000 steps, an additional
527 chain length of 50,000 steps and a thinning interval of 10 steps. Priors for a were
528 drawn from a non-informative uniform distribution from 0 to 10^6 , for b from a
529 uniform distribution from -1 to 1, and for σ^2_E and τ^2 from an inverse gamma
530 distribution with scale and shape equal to 0.001. As with our linear trend models,
531 chain convergence diagnostics were performed through visual inspection and the
532 Gelman and Rubin convergence diagnostic⁵⁹. Data for downstream analyses of
533 population stability only included estimates for routes that reached proper
534 convergence.

535
536 For both linear trend and density dependence hierarchical models, we excluded
537 species that typically pose clear challenges to detection, such as aquatic (families
538 Gaviidae, Podicipedidae, Pelecanidae, Phalacrocoracidae, Anhingidae, Anatidae,
539 Rallidae, Ardeidae, Threskiornithidae, and Ciconiidae), nocturnal (families
540 Tytonidae, Strigidae, and Caprimulgidae), and primarily aerial species (families
541 Apodidae and Hirundinidae). For all other species, we summarized regional
542 measures of population stability into a single species-specific value by computing
543 density-weighted averages across BCRs (linear trend models) or routes (density
544 dependence models). Thus, our measures of population variability account for
545 differences in population dynamics across a species' range⁶⁰, but place greater
546 importance on the population dynamics that occur in regions or sites where the
547 species is better represented.

548 549 *Estimating correlates of population stability*

550 Data on longevity and annual reproductive output were obtained from Myhrvold et
551 al. 2015⁵¹ (the latter was calculated as the product of clutch size and clutches per
552 year). Social systems were classified as either cooperative or non-cooperative
553 breeding based on Jetz and Rubenstein, 2011⁶¹. Habitat generalism was measured
554 as the number of different BCRs in which a species was reported throughout the
555 BBS dataset. Migratory status was determined from range maps by BirdLife
556 International (birdlife.org, downloaded March 18th, 2016). Specifically, a species
557 was considered resident if there was complete overlap between winter and
558 breeding portions of its range and considered migratory otherwise.

559

560 To test the effects of putative predictor variables on population stability scores we
561 used phylogenetic generalized least squares regression models estimated with the
562 'geiger'⁶² and 'nlme'⁶³ packages in R⁶⁴. All regression models (including the one used
563 to estimate relative brain sizes) were computed using Pagel's λ transformation. To
564 account for uncertainty in phylogenetic relationships, every regression model
565 reported here was independently ran with 1,000 different tree topologies from Jetz
566 et al.²⁷. Model fit was assessed through adjusted R-squared⁶⁵. In the main text we
567 report the average estimated coefficient for each parameter and the proportion of
568 trees in which such estimates were significant (i.e., the f statistic). Body size,
569 longevity, annual reproductive output, and estimated mean abundance were log-
570 transformed prior to analysis. Our fully parameterized models included all main
571 effects as well as interactions between longevity, annual reproductive output,
572 habitat generalism, body size, relative brain size, sociality, and migration with H1².
573 Models were subsequently reduced by iteratively removing, one at a time, terms
574 with the highest p-value (removing interactions prior to main effects) and assessing
575 whether removal led to a significant improvement of AIC values (i.e., $\Delta AIC > 2$). We
576 also computed variance inflation factors for all of our reduced models to confirm
577 low potential for multicollinearity (all VIF values were < 2).

578

579 *Estimating evolutionary rates of transition between character states*

580 We investigated the potential timeline of evolution of encephalization and climactic
581 niche in birds using models of correlated trait evolution⁴², implemented through the
582 discrete function of BayesTraits v2 on a global sample of species (Supplemental
583 Data 2). Pelagic and migratory species were excluded from these analyses, resulting
584 in a total sample of 1,288 resident terrestrial species. BayesTraits estimates the
585 eight possible transition rates between potential character states (see Fig. 3c or f),
586 assuming that simultaneous transitions in both brain size and environment are so
587 unlikely that they can be ignored⁴². Because both brain size and environmental
588 variability are continuous variables, we explored a number of different cutoff values
589 to convert them into binary traits suitable for this kind of analysis. Specifically, we
590 classified species as having large encephalization values when they occurred above
591 the 30th, 50th, 75th and 90th percentile of brain size distribution. While a 30th
592 percentile cutoff for encephalization may seem too permissive at first glance, we
593 note that this was the minimum possible threshold at which all "large-brained"
594 species had a positive brain residual (i.e., bigger brain than expected from body
595 size) and the number of observed transitions between different states was sufficient
596 for the proper estimation of transition rates⁶⁶. We note that the skewed distribution
597 towards more highly encephalized species in our sample is due to the effects of
598 phylogenetic correction in the estimation of relative brain size, as well as to the
599 subsampling of species from our much larger global brain data set. Exposure to
600 environmental variability was classified as high for species above the 50th, 75th, and
601 90th percentiles in either 'temperature variability' or 'xeric variability'. Because
602 models of correlated trait evolution have the potential to identify spurious
603 correlations when the number of transitions between states is low⁶⁶, we began by
604 confirming that all of our thresholds yielded a reasonable number of transitions
605 between states using ancestral character state estimation via the R package

606 'phytools'⁶⁸ and averaging the detected number of transitions across 1,000 tree
607 topologies. At the 30th percentile threshold we detected an average of 29 transitions
608 from small to large encephalization and 65 transitions from large to small
609 encephalization. At the 50th percentile threshold we detected an average of 102
610 transitions from small to large encephalization, 112 transitions from large to small
611 encephalization, 253 transitions from stable to variable environments, and 414
612 transitions from variable to stable environments. At the 75th percentile threshold we
613 detected an average of 64 transitions from small to large encephalization, 36
614 transitions from large to small encephalization, 265 transitions from stable to
615 variable environments, and 195 transitions from variable to stable environments.
616 Finally, at the 90th percentile threshold we detected an average of 46 transitions
617 from small to large encephalization, 15 transitions from large to small
618 encephalization, 237 transitions from stable to variable environments, and 127
619 transitions from variable to stable environments. The 90th percentile threshold was
620 therefore ultimately dropped as a criteria for dichotomizing encephalization
621 because the low number of transitions it yielded would preclude any meaningful
622 estimates of transition rates⁶⁷.

623
624 Rates of evolutionary transition were estimated using reversible-jump Markov
625 Chain Monte Carlo analyses (rjMCMC). Parameter values were first estimated using
626 maximum likelihood analysis in order to inform our choice of priors. For all six
627 combinations of cutoffs, we calculated mean values of transition rates across our
628 sample of 1,000 trees. Maximum likelihood estimates of each parameter value were
629 of a similar magnitude regardless of cutoffs and ranged from 0.00002 to 0.34. Next,
630 rjMCMC analyses were performed for 200,000,000 iterations with a burnin of
631 5,000,000, a thinning interval of 1,000 iterations, and an exponential prior whose
632 mean is seeded from a uniform hyperprior ranging between 0 and 0.5. Reversible-
633 jump helps avoid model over-parameterization by exploring alternative models that
634 can differ in parameter number⁶⁹. Because reversible-jump analyses estimate the
635 posterior probability of all possible model configurations along with individual
636 parameter values, this algorithm offers the additional advantage of enabling tests of
637 very specific hypothesis. Specifically, the posterior distribution of model types
638 obtained through rjMCMC can be used to assess the strength of evidence that two
639 particular transitions are different or not by comparing the relative sampling
640 frequency of models in which the two transition types were constrained to be the
641 same with that of models in which these two rates were allowed to vary
642 independently of each other⁷⁰. Statistically, these comparisons are made via Bayes
643 factors, which are calculated as:

644
645
646

$$BF_{ij} = P(M_i|D)/P(M_j|D) \times P(M_j)/P(M_i),$$

647 where i is the model set where rates are allowed to vary independently, j is a
648 reduced model set in which the two rates are constrained to be the same, $P(M_n|D)$ is
649 the posterior probability of model set n (computed as the proportion of steps in
650 which the chain visited model n), and $P(M_n)$ is the prior probability of model set
651 n ^{69,70}. For example, when testing the cognitive buffer hypothesis, $P(M_i|D)$ is the

652 frequency of all model configurations within the posterior distribution in which the
653 transition rate from moderate to large encephalization varied between stable and
654 variable environments, whereas j includes all model configurations in the posterior
655 distribution where these rates were constrained to be equal in both environments.
656 Similarly, when testing the colonization advantage scenario, $P(M_i|D)$ is the
657 frequency of all model configurations in which the transition rate from stable to
658 variable environments varied between moderate and large encephalization, while j
659 includes all configurations where these rates were constrained to be equal in both
660 brain size classes. $P(M_n)$ values for this formula are computed by exploring all
661 possible model combinations via expanded Stirling numbers⁷⁰: $P(M_j) = 0.9592$ and
662 $P(M_i) = 0.0408$. Overall, resulting Bayes factor values from 3 to 12 suggest positive
663 support for model set i and values above 12 suggest that model set i is strongly
664 supported when compared to model set j ⁶⁹. We also report the proportion of steps
665 in our model chains (P) in which the difference between two rates of interest was
666 equal to zero (*i.e.*, the transition rate for the character of interest was independent
667 of the state of the second trait). In this case, values of $P < 0.014$ indicate positive
668 support for a difference between rates (*i.e.*, $BF > 3$)⁷⁰. Because hypothesis testing
669 directly assesses the proportion of steps in the posterior distribution where
670 transition rates of interest are constrained to be equal, we visualize these results by
671 plotting the distribution of ‘rate differences’ calculated across the posterior
672 distribution. These rate differences were calculated at each step of the chain as
673 either the difference in estimated transition rate from moderate to large brain sizes
674 in variable versus stable environments (when testing the cognitive buffer
675 hypothesis), or the difference in estimated transition rates from stable to variable
676 environments in species with large versus moderate brain sizes (when testing the
677 colonization advantage hypothesis). Plotting the distributions of rate differences
678 (figure 3) allows us to assess both the support for a particular hypothesis (the
679 proportion of steps where rate difference = 0) and the directionality of these
680 potential differences. Besides explicitly testing the cognitive buffer and colonization
681 advantage scenarios as indicated above, we also tested for differences in the rates of
682 colonization of stable environments between brain size classes as well as for
683 differences in the rate of evolution of small to moderate brain sizes in stable versus
684 variable habitats.

685
686 We ran each rjMCMC analysis three times to insure chain convergence and assess
687 the consistency of our results. These checks were performed with the ‘coda’ package
688 in R⁵⁹ and included visually inspecting the traces of all of our posterior estimates,
689 assuring effective sample sizes were greater than 1000, and estimating potential
690 scale reduction factors (PSRF) using Gelman and Rubin’s convergence diagnostic⁶⁰.
691 PSRF values were below 1.1 for all parameter estimates indicating proper chain
692 convergence properties. Effective sample sizes over 1000 were obtained for all runs,
693 except for analyses using the combination of 50th percentile encephalization
694 threshold and 75th percentile environment threshold. To ensure consistent results
695 for this cutoff, we performed three additional runs for 619,000,000 iterations (the
696 upper limit of our current computational resources). While 4 rate parameters in
697 these models still failed to reach target effective sample sizes of 1,000 during the

698 extended runs, their effective sample sizes were nevertheless fairly high (range:
699 371-997). Furthermore, the plots of running values across iterations for Bayes
700 Factors testing the cognitive buffer and colonization advantage hypotheses in these
701 models, indicate that these results are also highly stable (Supplementary Fig. 2).
702 Posterior distributions of parameter estimates from the different chains produced
703 for each threshold were subsequently pooled to calculate both the mean values and
704 standard deviations for each transition rate (Supplementary Fig. 3).

705

706 *Ancestral trait reconstruction*

707 The ancestral states reported in Fig. 4 were reconstructed for visualization purposes
708 only, and estimated with the 'phytools'⁶⁸ package in R. Reconstructions of
709 continuous trait data were based on maximum likelihood and a randomly chosen
710 tree within our candidate set. Color-coding in figure 4b-g is based on results from
711 separate ancestral trait reconstructions for the different environmental variables.

712

713 *Data availability*

714 All data generated or analyzed during this study are either available through cited
715 sources or included in this published article and its supplementary information files.

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892

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900

901 **Author Contributions**

902 T.S.F. and C.A.B. designed analyses, compiled data, and wrote the manuscript. T.S.F.
903 additionally performed analyses and prepared figures. A.N.I. collected and compiled
904 data and contributed to writing.

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907 **Competing Financial Interests**

908 The authors declare no competing financial interests

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Tables

Table 1. Summary of principle component analysis of environmental variables across North American.

	Loadings*		Uniqueness
	PC1	PC2	
Temperature predictability	0.84	0.17	0.27
Temperature variance	-0.82	-0.26	0.26
log (precipitation variance)	0.79	0.40	0.21
Mean temperature	0.75	0.51	0.18
Precipitation predictability	-0.71	0.41	0.33
sqrt NPP variance	-0.05	0.94	0.11
log (mean NPP)	0.28	0.93	0.06
NPP predictability	-0.56	-0.76	0.11
log (mean precipitation)	0.57	0.65	0.25
Cumulative variance	0.42	0.80	

940 * Loadings for main contributors to each component are in bold.

941 **Table 2.** Summary results of our phylogenetic generalized least squares regression
 942 models of population stability across a sample of 1,000 potential tree topologies for
 943 the avian phylogeny*.

Predictor	$\bar{\beta}$	\overline{SE}	\bar{t}	\bar{p}	f^\dagger
(Intercept)	-0.17	0.07	-2.32	0.02	1.00
H1 ^{2‡}	0.06	0.04	1.67	0.10	0
Relative brain size	-0.01	0.05	-0.22	0.82	0.00
Migration	-0.03	0.03	-1.31	0.19	0.00
log(Longevity)	0.03	0.02	1.30	0.20	0.00
Migration:H1 ²	0.05	0.01	3.60	< 0.001	1.00
log(Longevity):H1 ²	-0.06	0.01	-3.90	< 0.001	1.00
Relative brain size:H1 ²	0.08	0.02	4.91	< 0.001	1.00

df = 118 $\lambda = 0.60$

944 * Only terms present in the final reduced model are presented here (see text for
 945 details). Coefficient estimates (β), standard errors (SE), t-scores, and significance
 946 levels reported are averages for 1,000 model runs with randomly selected
 947 phylogenetic trees based on the Hackett backbone in Jetz et al.²⁷.

948 † f is the frequency of trees for which p -values were < 0.05.

949 ‡ H1² is the quadratic term of composite measure, H1, which captures various
 950 aspects of environmental variability. Low values of H1 represent cold seasonal
 951 habitats with unpredictable temperatures; high values represent warm habitats
 952 characterized by variable and unpredictable patterns of precipitation.

953

954 **Figures**

955

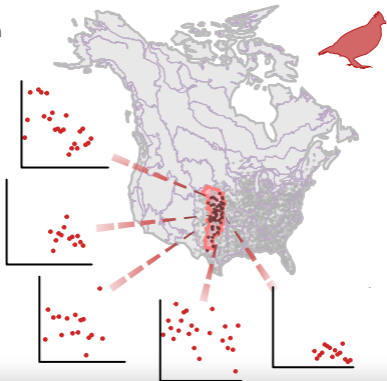
956 **Figure 1: Graphical representation of our method for estimating and**
957 **comparing population dynamics of North American birds.** Population dynamics
958 were first estimated independently for every species, here the Northern bobwhite
959 (*Colinus virginianus*), in every North American conservation region (outlined in
960 purple), and subsequently reduced to individual weighted averages per species. **a,**
961 Data come from counts (shown as inset plots) reported at routes (depicted as dots
962 on the map) within conservation regions (outlined in purple). **b,** Models estimate
963 the log of abundances that follow a general long-term trend (dark red line) and
964 yearly fluctuations around the trend (light red line) that that are drawn from a
965 normal distribution with mean of 0 and standard deviation of σ_γ .
966

967 Figure 2: **Significant two-way interactions between species traits and**
968 **environmental variability on population stability.** **a-c**, Partial residual plots from
969 phylogenetic generalized linear model with fitted lines indicating the effect of
970 environmental variability on population stability for different migratory strategies
971 (**a**) and at different values of longevity (**b**), and relative brain size (**c**) in a sample of
972 126 species of North American birds. Environmental variability is measured H1,
973 with low values indicating cold, seasonal habitats with unpredictable temperatures,
974 and high values indicating hot habitats with variable and unpredictable
975 precipitation patterns (see text and Table 1). Traits in **b-c** were analyzed as
976 continuous variables but, for visualization purposes, the fitted lines depicted here
977 predict population stability trends for species at the 5th, 25th, 50th, 75th, and 95th
978 percentiles of each focal trait while holding all other predictors at their mean value
979 and setting migratory status as resident.
980

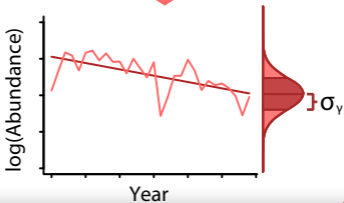
981 **Figure 3: Testing the sequence of evolutionary events predicted by the**
982 **cognitive buffer and colonization advantage hypotheses.** The cognitive buffer
983 hypothesis predicts that larger brains should preferentially evolve in variable
984 environments, whereas the colonization advantage hypothesis predicts that, once
985 evolved, they should subsequently aid in colonizing variable habitats. **a and d,**
986 Posterior distributions of the difference in transition rate from moderate to large
987 encephalization in stable vs variable climates (depicted by blue arrows in **c and f**). **b**
988 **and e,** Posterior distribution of the difference in transition rate from stable to
989 variable environments in moderate vs large brained species (depicted by green
990 arrows in **c and f**) estimated from a sample of 1,288 resident terrestrial bird species
991 from around the globe. Distributions in **a, b, d,** and **e** are derived from the posterior
992 distributions of reversible-jump MCMC analyses (see Supplementary Fig. 3).
993 Positive values indicate support for a particular hypothesis (see methods).
994 Horizontal red lines in these panels mark the maximum proportion of steps in which
995 the rjMCMC chain can visit a rate difference of 0 while still supporting a scenario in
996 which the two rates of interest differ (i.e., Bayes Factor = 3). Thus, we see positive
997 support for difference in transition rates in **a, b,** and **e** but not in **d. c and f** depict the
998 full transition matrices summarizing estimated rates of transition between stable
999 (gray) and variable (black outlined) environments or between moderate (purple)
1000 and big (pink) relative brain size. Arrow widths are proportional to estimated rates,
1001 single asterisks indicate positive support for a difference between rates (BF > 3),
1002 and double asterisks indicate strong support for a difference between rates (BF >
1003 12).
1004

1005 Figure 4. **Ancestral trait reconstruction of relative brain size and**
1006 **environmental niche. a**, phylogeny of the 1,288 species in our global sample
1007 depicting the reconstructed ancestral states of avian encephalization. **b-g**,
1008 reconstruction details for 6 highly encephalized clades: encephalization (left panels;
1009 pink = upper 25th percentile; grey = lower 75th percentile) and variable
1010 environmental niches (right panels; blue = upper 25th percentile of 'temperature
1011 variability'; yellow = upper 25th percentile of 'xeric variability'; black = upper 25th
1012 percentile for both measures; grey = bottom 75th percentile for both measures).
1013 Subtrees in panels **b-g** are details of reconstructions performed on continuous trait
1014 data with branches re-colored based on the 75th percentile threshold used in
1015 analyses of correlated trait evolution (see methods).

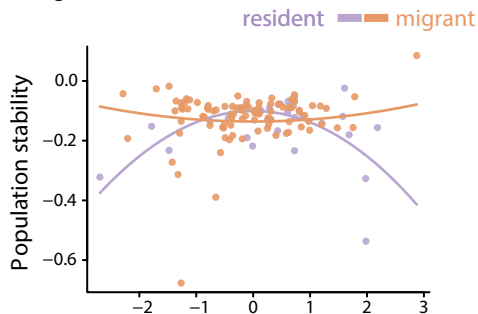
a



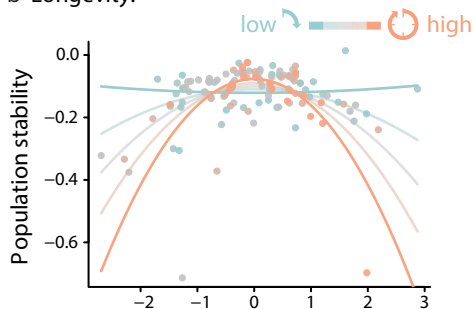
b



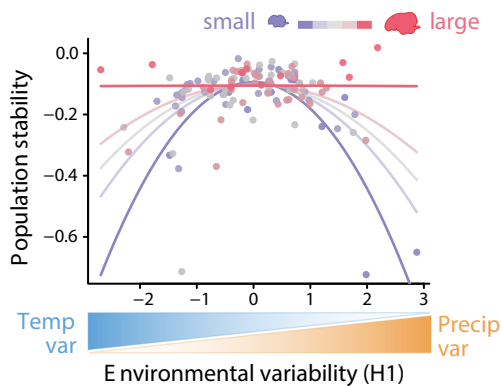
a Migration:



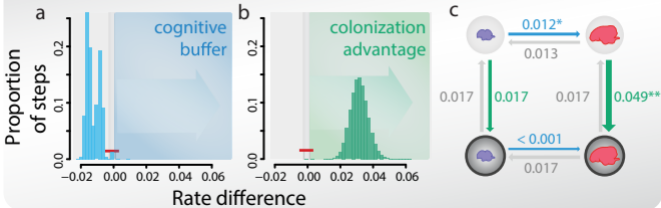
b Longevity:



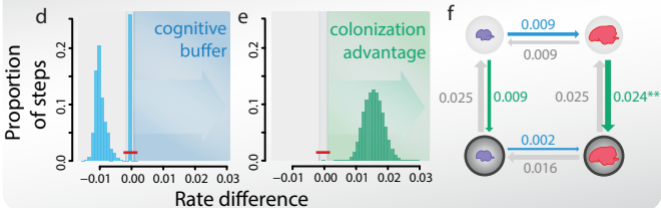
c Relative brain size:

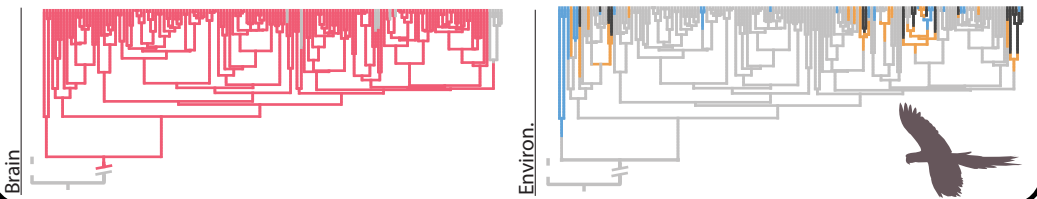
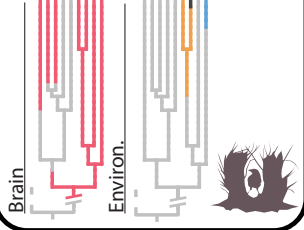
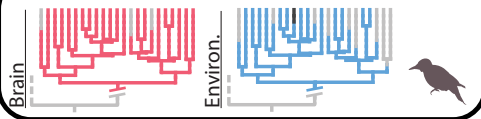
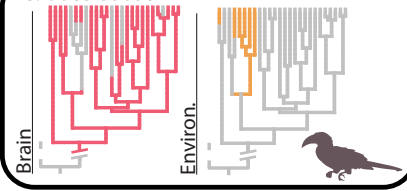
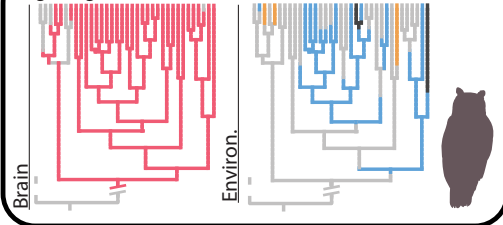


Thresholds: 50th percentile Brain; 50th percentile environment



Thresholds: 50th percentile Brain; 75th percentile environment



b. Psittaciformes**c. Ptilonorhynchidae****d. Picidae****e. Bucerotidae****g. Strigidae**

Small Large
Relative brain size

Moderate Large
Brain

Stable Variable
Environment
tv
tv + xv
xv

f. Corvidae