

1 **Habitat structure drives the evolution of aerial displays in birds**

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3 João C. T. Menezes^{1,2*} & Eduardo S. A. Santos^{1,2}

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5 *¹Programa de Pós-graduação em Ecologia, Universidade de São Paulo, 05508-090, São Paulo,*

6 *Brazil*

7 *²BECO do Departamento de Zoologia, Universidade de São Paulo, 05508-090, São Paulo,*

8 *Brazil*

9 **Corresponding author: jocateme@gmail.com*

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11 **Physical properties of the environment may shape signalling traits by determining**

12 **how effective the signals are in affecting the behaviour of other individuals.**

13 **Evidence abounds of signalling environment driving the evolution of colours and**

14 **sounds, but little is known about its influence upon gestural displays. Here, we**

15 **performed a continent-wide phylogenetic comparative analysis to test the**

16 **hypothesis that habitat structure drives the evolution of aerial sexual displays in**

17 **passerine birds. We found that aerial displays are seven times more likely to evolve**

18 **in open habitats than in forests, likely as a result of physical properties that allow**

19 **aerial displays to transmit more broadly in open habitats. Our results provide an**

20 **emblematic example of how environmental factors may help predict the direction of**

21 **evolution of otherwise unpredictable sexual traits. The broader range of aerial**

22 **displays in open habitats may also mean that females can sample more males,**

23 **potentially leading to more intense sexual selection over open-habitat, aerial-**

24 **displaying males.**

25

26 Communication in animals occurs through the emission and reception of signals –
27 acts or structures that, by definition, have been selected because they affect the
28 behaviour of other organisms^{1,2}. How effectively a particular trait affects the behaviour
29 of another organism, however, depends upon the physical properties of the
30 environment through which the signal is transmitted³. For instance, females of three-
31 spined sticklebacks (*Gastosteus aculeatus*) prefer mates that have a brighter-red
32 coloration⁴. Red coloration in males, thus, is a signal: it has been selected because it
33 affects how females choose a mate. However, under green artificial light, red coloration
34 is not transmitted as effectively and thus females show no preference⁴. If a hypothetical
35 population of sticklebacks had lived under green lighting conditions all along their
36 evolutionary time, red coloration would most likely not be selected as a signal of male
37 quality. Such influence of environmental properties upon both ends of communication
38 systems – signalling trait and sensory tuning to receive it – is the key feature
39 underlying the sensory drive hypothesis^{3,5,6}. As a consequence, we can expect the same
40 characteristic to be positively selected in some environments, but not in others.
41 Accordingly, the structure of many signals has been found to be habitat-dependent in
42 animals that use colours, sounds, ornaments or vibration to communicate (reviewed in
43 ^{3,7}). However, empirical evidence of sensory drive upon gestural (motion-based)
44 signals (henceforth, displays) is mostly restricted to individuals adjusting their
45 behaviour to maximize the conspicuousness of the display – for example, by choosing
46 an appropriate signalling site or timing⁸⁻¹³.

47 Various animals, from jellyfishes¹⁴ and arthropods¹⁵⁻¹⁷ to aquatic and terrestrial
48 vertebrates¹⁸⁻²⁴, use gestural displays as sexual signals. These displays are selected
49 through intersexual mate choice or intrasexual competition mechanisms^{25,26} and may,
50 as any signal, be subject to selective pressures imposed by the signalling environment.
51 Only recently, however, have researchers begun to look into the potential influence of

52 the environment upon the structure of displays – rather than the choice of timing or
53 site –, with two studies finding evidence of it^{27,28}. Thus, we currently have tentative
54 knowledge about the influence of the signalling environment on the evolution of
55 gestural displays.

56 Sexual displays performed by passerine birds come in all forms: from the
57 simple, static ‘bill-up’ posture of silver-beaked tanagers (Isler & Isler 1987 *in* ²⁹) to the
58 most complex, skilful dances performed by manakins³⁰ and birds-of-paradise²⁸.
59 Passerines also exhibit high variability in habitat preferences, having colonized
60 environments as diverse as Arctic tundras, tropical rainforests and arid deserts³¹. These
61 features make Passeriformes a promising group to investigate the potential role of
62 environment in shaping displays. As we will argue, a particular component present on
63 many of the sexual displays exhibited by passerines – the flight component of aerial
64 displays – seems particularly likely to evolve under sensory drive. For example, flying
65 above an open habitat (*vis-à-vis* underneath the forest canopy) during the display puts
66 the signaller under more intense light³², and, as a consequence, the signal reaches a
67 wider range of potential receivers, all else held constant³³. Moreover, flying above an
68 open habitat may result in less or no vegetation obstructing the signaller from the
69 perspective of potential receivers. Flying inside the forest does not reduce visual
70 obstacles between signaller and receivers and, in addition, the display is less likely to
71 be perceived the farther signaller and receiver are because vegetation accumulates
72 horizontally. Lastly, complex visual backgrounds make signals less consistently
73 perceived⁹. The sky is as uniform as a background may be, while forest interior is a
74 highly heterogeneous one.

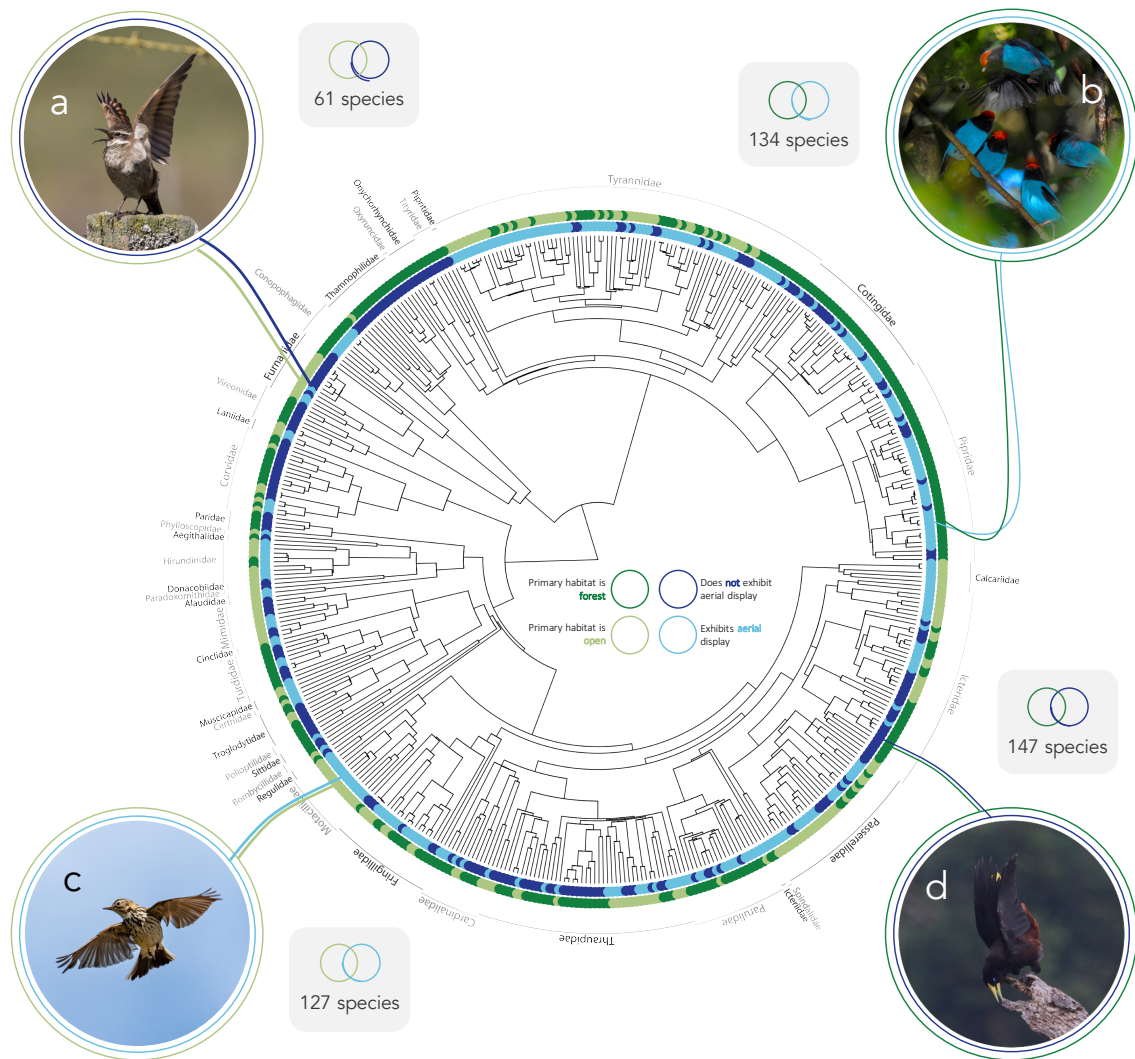
75 Thus, although females may assess motor performance of males from a short
76 distance in both habitats²⁶, it is unlikely that aerial displays offer any advantage in a
77 broader spatial scale in forests. In open habitats, a flight component may allow the

78 display reach a broad range of potential receivers with more intensity, less visual
79 obstruction, and more consistency. Here, we evaluated whether sensory drive
80 influences the evolution of sexual displays by testing the hypothesis that aerial
81 displays are more likely to evolve in passerine birds that inhabit open habitats than in
82 those that inhabit forests. We did that by performing a continent-wide phylogenetic
83 analysis of 469 species, which constitutes the most comprehensive test of sensory drive
84 – phylogenetically and geographically – as far as we are aware. If our findings
85 support this hypothesis, we would provide evidence to corroborate, for the first time,
86 the pattern predicted for decades by researchers^{34–36}, but never actually tested, that
87 aerial-displaying species are more prevalent in open habitats than in forests.

88 **Results**

89 We were able to collect data about sexual display and primary habitat structure for 469
90 (19.2%) species of New World passerines belonging to 41 families (Supplementary
91 Data); the remaining species – for which data was not available – were excluded
92 from analyses. Each species was classified as to the *presence* (1) or *absence* (0) of aerial
93 sexual display, and as living primarily in *open habitats* (1) or *forests* (0). Among open-
94 habitat passerines, 127 of 188 species (68%) were aerial displayers, whereas 48% ($N =$
95 134) of the 281 forest species exhibited aerial display (Figure 1). Although this pattern
96 is consistent with the common perception that aerial-displaying passerines are more
97 prevalent in open habitats, it allows no inference as to whether habitat influences the
98 evolution of aerial display.

99



100

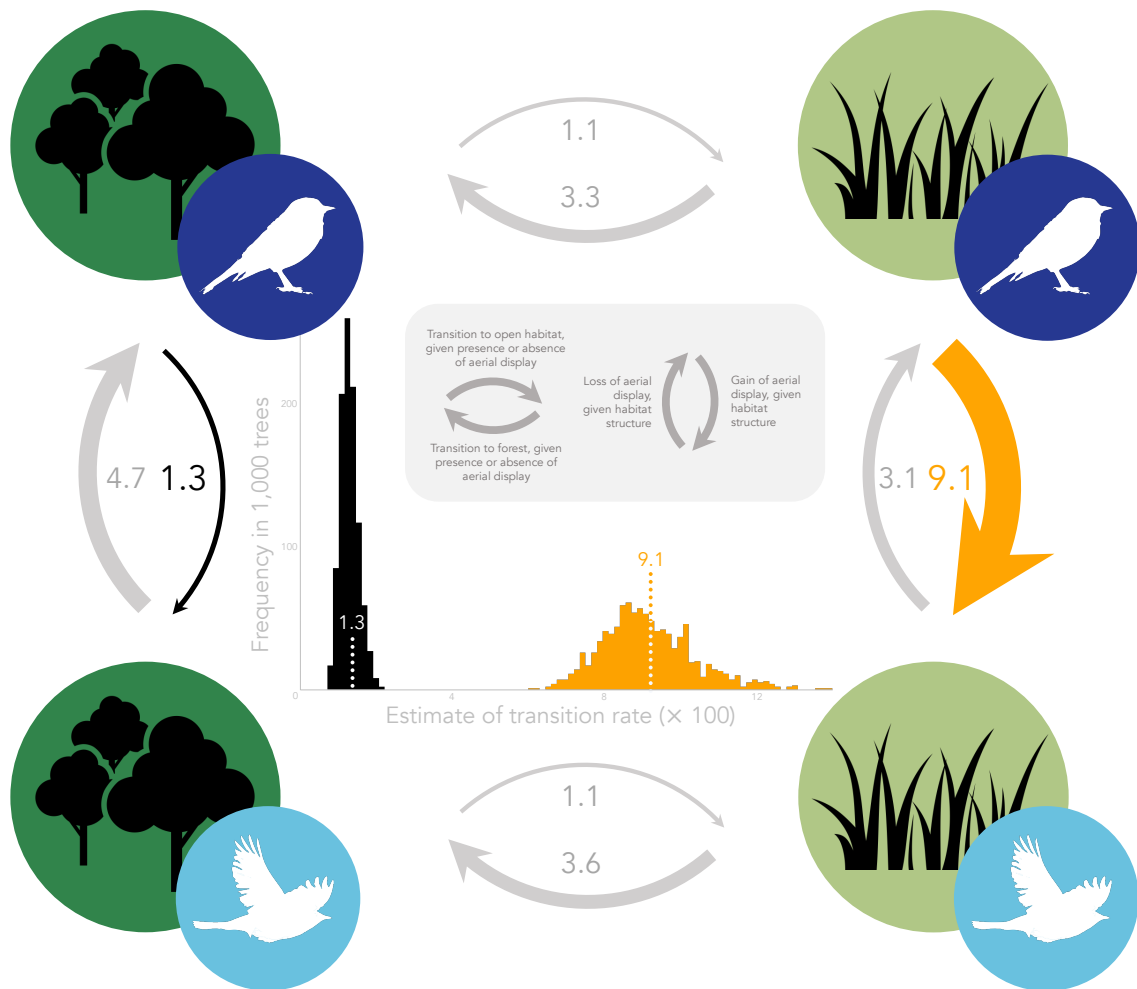
101 **Figure 1.** Phylogenetic distribution of display and habitat structure data (inner and
 102 outer circle, respectively), number of species (grey boxes) and examples of species in
 103 each category: (a) stout-billed cinclodes (*Cinclodes excelsior*) exhibit non-aerial display
 104 in open habitats (photo courtesy of Ken Chamberlain), (b) blue manakins (*Chiroxiphia*
 105 *caudata*) exhibit aerial display in forests (photo courtesy of João Quental), (c) meadow
 106 pipits (*Anthus pratensis*) exhibit aerial display in open habitats (photo courtesy of Kevin
 107 Hay), and (d) crested oropendolas (*Psarocolius decumanus*) exhibit non-aerial display in
 108 forests (photo by Gregory Smith, CC BY-SA 2.0). For the ancestral state estimation, see
 109 Figure S1.

110

111 To test the hypothesis that aerial displays are more likely to evolve in open-
112 habitat passerines than forest ones, we conducted two different phylogenetic
113 comparative analyses using species-level Passeriformes trees³⁷. In the first analysis, we
114 fitted phylogenetic logistic regression models (PLogReg³⁸) to determine whether
115 habitat structure influences the probability that a species exhibits aerial display, while
116 accounting for phylogenetic dependence among species. We compared a null model
117 (with no predictor variable) with one in which habitat structure was fit as a categorical
118 predictor, and accounted for phylogenetic uncertainty by running each model with a
119 sample of 1,000 topologies, and performed model choice using the Akaike information
120 criterion (AIC). The model containing habitat structure as a predictor was selected in
121 all of the 1,000 iterations, with a mean Δ AIC of 17.56 (min = 6.11, max = 46.23). Mean
122 slope estimate for open habitat was 0.489 (95% CI: 0.485 to 0.492), with a mean p -value
123 of 0.025 (≤ 0.05 in 92.8% of iterations). This indicates that the probability that a
124 passerine species exhibits an aerial sexual display is greater in open habitats than in
125 forests. Performing this analysis with a Bayesian (MCMC) approach yielded
126 qualitatively similar results (see Supplementary Results). We performed an additional
127 PLogReg to test whether forest stratum influences the probability that forest passerines
128 exhibit aerial display, but found no clear effect (see Supplementary Results). This result
129 does not support the idea that canopy stratum acts in a similar way as open habitats in
130 terms of signal transmission properties.

131 Secondly, we fitted a series of Markov models^{39,40} to test for correlated
132 evolution between aerial display and habitat structure using the same set of species
133 and trees. We designed four biologically plausible models: a) independent (habitat
134 transitions not depending on aerial display state and vice-versa), b) correlated (each
135 variable depending on the other), c) habitat-dependent (aerial display transitions
136 depending on habitat state), and d) display-dependent (habitat transitions depending

137 on aerial display state). We fitted each model using maximum-likelihood estimates and
138 extracted their AIC value. We predicted that the habitat-dependent model would be
139 the best in the model set to explain our data, as habitat should influence the probability
140 of gaining or losing aerial display, but exhibiting or not aerial displays should not
141 influence transitions between habitats. Indeed, the habitat-dependent model had the
142 lowest AIC in 98.3% of the trees (max. $\Delta\text{AIC} = 1.50$; Figure S2). However, the weight of
143 evidence in its favour was not unequivocal⁴¹ (*i.e.*, Akaike weight, $w_i \leq 0.90$) in 92.5% of
144 the trees (median = 0.84; range = 0.32 to 1.00), with the correlated model having a
145 weight of evidence as high as 0.68 (median = 0.15; Figure S3). For this reason, and to
146 avoid having to use subjective ΔAIC thresholds to select a single best model, we
147 decided to perform model averaging of the estimates. We did that by weighting the
148 transition rates estimated in each of the four models by the model's Akaike weight,
149 resulting in a single model-averaged estimate of each transition rate per tree (Figure
150 S4). We then evaluated these transition rate estimates to evaluate whether gains of
151 aerial display are more likely in open habitats than in forests. Across the 1,000 trees, we
152 found that transition rates to aerial displays are 7.03 ± 1.28 (median \pm SD) times more
153 likely in open habitats than in forests, as predicted by our hypothesis (Figures 2, S5).
154



155

156 **Figure 2.** Evolutionary transition rates between habitat structure and aerial display.

157 Arrows are weighted by the values beside them, which indicate the median ($\times 10^2$)

158 model-averaged maximum-likelihood estimate of each rate across 1,000 different trees.

159 Median transition rates to aerial displays are approximately seven times higher in open

160 habitats (orange arrow) than in forests (black arrow; see Figure S5 for the distribution

161 of orange rate to black rate ratios). In the centre, distribution of estimates of the two

162 rates of interest across the 1,000 trees (see Figure S4 for the distribution of estimates of

163 all transition rates).

164 Discussion

165 Our findings support the hypothesis that aerial displays are more likely to evolve in

166 open-habitat passerines than forest ones. This macroevolutionary pattern is likely the

167 result of physical properties of the environment that allow aerial displays to transmit
168 more broadly and effectively in open habitats than forests. Therefore, our order-level
169 analysis of 469 species provides the most comprehensive evidence of sensory drive
170 acting on signal evolution to date, as far as we are aware. It is also the first
171 phylogenetic analysis to find evidence of habitat shaping the evolution of gestural
172 displays. Previous studies had recognized the role of habitat structure in shaping
173 sound-, colour- and ornament-based signals in lizards and birds⁴²⁻⁴⁷, but failed to
174 detect an influence of habitat on the structure of motion-based signals (*e.g.*, in fiddler
175 crabs¹⁶). More than seven decades after Armstrong's³⁴ (p. 247) remark that "high-flying
176 [...] displays are most characteristic of birds of the open country", we offer compelling
177 evidence of the evolutionary process that likely underlies this pattern. Armstrong then
178 goes on to state that the "prime consideration [of display-flights] is to attract the
179 attention of the immigrant females". Indeed, all displays analysed in our study
180 likewise have a sexual function. Therefore, the fact that these are sexual displays allows
181 us to discuss how our findings about sensory drive may interact with sexual selection,
182 particularly regarding its direction and intensity.

183 Classical sexual selection models such as Fisherian runaway⁴⁸⁻⁵⁰ and
184 handicap^{51,52} offer little prediction about which sexual traits should evolve and to what
185 direction⁵³. The handicap model, for instance, predicts how costly a signal should be,
186 but not how these costs should be expressed⁵⁴. The Fisherian runaway process assumes
187 an arbitrary direction of evolution altogether^{55,56}. Passerine gestural displays may seem
188 particularly unpredictable, with multiple, clade-specific evolutionary forces acting on
189 their evolution^{28,57,58}. Yet, here we show that a simple ecological factor, habitat
190 structure, predicts to a great degree the presence of a major gestural component. In the
191 paper introducing the sensory drive hypothesis, Endler⁵ highlighted an important
192 aspect of sensory drive: that it allows us to predict which specific sexual traits should

193 evolve as signals and to what direction. Our findings provide an emblematic example
194 of how the signalling environment may help predict the direction of evolution of
195 sexual signals.

196 Our system also allows us to explore the interplay between sensory drive and
197 sexual selection from a different perspective. The effectiveness of aerial displays is
198 influenced by the habitat because the signal can reach a broader range in open habitats
199 than in forests. For males, this means that a male performing aerial display is able
200 reach a higher number of females in open habitats than in forests. From the female
201 perspective, it means that females are able to assess more males per unit of time in
202 open, unobstructed habitats, thus increasing the number of potential mates they can
203 sample during the mate choice process. Recent comparative and simulation data show
204 that when females can sample more males during mate choice, sexual selection is
205 stronger and, consequently, male ornaments are expected to be more extreme⁵⁹. Thus,
206 besides driving the evolution of aerial displays through sensory drive, we suggest that
207 open habitats may intensify sexual selection on male aerial displayers by enabling
208 females to sample more males in the population.

209 **Methods**

210 *Study group*

211 Passeriformes is, by far, the most speciose order of birds, encompassing 5,966 species³⁷
212 that show a diverse array of sexual behaviours and habitat-selection strategies³¹. Such
213 diversity, and the fact that Passeriformes have well-sampled phylogenies³⁷, make them
214 an appropriate group for the purposes of this study. We searched for information on
215 all extant species that regularly breed in the New World, excluding oceanic-island
216 endemics (*e.g.*, Hawaii, Galápagos and Juan Fernández). According to the American
217 Ornithologists' Union⁶⁰⁻⁶², 2,393 species meet these criteria, but an additional 49 species

218 are recognized by Jetz et al.³⁷, totalling 2,442 targeted species (Supplementary Data).
219 For each species, we answered the following questions, which brought forth the three
220 binary variables used in the analyses: (i) do individuals perform aerial display?; (ii) do
221 individuals occupy primarily open or forest habitats?; and, in the case of forest species,
222 (iii) do individuals forage exclusively in canopy stratum? Each of these variables will
223 be detailed below.

224

225 *Display data*

226 We collected display data from a variety of sources: life-history databases (*Handbook of*
227 *the Birds of the World Alive*³¹, accessed 19 December 2016–10 March 2018; Cornell Lab of
228 Ornithology's *Neotropical Birds Online*²⁹, accessed 21 August 2017–10 March 2018),
229 natural-history books (A. C. Bent's *Life histories of North American birds* series⁶³⁻⁷²; A. F.
230 Skutch's *Life histories of Central American birds*⁷³⁻⁷⁵; A. Wetmore's *The birds of the republic*
231 *of Panama*^{76,77}; H. Sick's *Ornitologia brasileira*³⁵), an online media database (HBW's
232 *Internet Bird Collection*, <http://hbw.com/ibc>, accessed 4–10 October 2017) and a data
233 paper⁷⁸ (see Supplementary Methods for details).

234 For data collection purposes, we considered sexual display any ritualized,
235 sexually selected gesture or posture. The question *do individuals perform aerial display?*
236 was answered *yes* (1) for a species only if any of the data sources claimed that
237 individuals perform a sexual display that includes a flight component (*i.e.*, an aerial
238 display). Otherwise, it was answered *no* (0) if any source claimed either (a) that
239 individuals do not perform aerial sexual display, or (b) that they perform sexual
240 display that does not include a flight component. Note that, for this question to be
241 answered – be it with a yes or a no – a sexual display must have been mentioned by
242 at least one data source (lack of any mention would result in NA). We used a set of
243 criteria to infer from the available information whether a display is sexual (*i.e.*, sexually

244 selected) and thus relevant for data collection purposes (Table 1). For some species (N
245 = 29), information was ambiguous about whether the mentioned displays were sexual
246 (see Table 1 for what we considered ambiguous). We excluded the ambiguous species
247 from the analyses in the main text, but we also ran a phylogenetic logistic regression
248 including them to assess whether it would change the results; it did not (see
249 Supplementary Results).

250 We defined flight component as the flapping of wings while the individual is
251 not perched. In our conception, aerial displays are only likely to be more effective in
252 open habitats if the flight is high enough that the bird surpasses the open vegetation. In
253 spite of that, we decided to adopt an inclusive definition of flight component – one
254 that includes even flights with little or no vertical gain – because for most species
255 there was no information about the height of flight during display. This decision is
256 likely conservative because most of the species with horizontal-flight displays we
257 know of are forest dwellers (e.g., *Conopophaga*, *Rupicola*, many Pipridae, *Mionectes*,
258 *Platyrrinchus*). For some species ($N = 9$), we were unable to determine with certainty
259 whether the sexual display included or not a flight component. This occurred when we
260 came across ambiguous descriptions such as “occasional jumps/leaps into the air”⁷⁸,
261 “flitting from twig to twig”⁷⁵ (p. 45), and “move restlessly from branch to branch”
262 (Mitchell 1957 *in* ²⁹). We dealt with such uncertainty by repeating analyses considering
263 flight component either absent (main results) or present (Supplementary Results) in the
264 display; the results were qualitatively similar.

265 Overall, we were able to determine whether 470–499 passerine species
266 (depending on how strict we were in treating a display as sexual) exhibited aerial
267 displays or not, which represents 19.2–20.4% of the initial sample set. The remaining
268 species were classified as NA and thus dropped from the analyses (this same decision
269 was applied to the other variables as well).

270

271 **Table 1.** Criteria used to infer whether a display described in the literature is sexual
 272 (*i.e.*, sexually selected) or not. For a display described in a given data source, if the
 273 available textual information matched any corresponding column below, display was
 274 considered to be sexual. For instance, for a display described in del Hoyo et al.³¹, IF
 275 explicit function is sexual, courtship, ... OR section is Breeding OR period of
 276 occurrence is predominantly during breeding period OR sex of performer or intended
 277 receiver is specific, THEN display was considered to be sexual. Footnotes refer to
 278 criteria that indicate that display may or may not be sexual; we repeated analyses
 279 including or excluding such displays (see Supplementary Results).

Source	Explicit function*	Section	Period of occurrence	Sex of performer or intended receiver
del Hoyo et al. ³¹		Breeding [‡]		
Schulenberg ²⁹		Sexual behavior [‡]		
Skutch ⁷³⁻⁷⁵	sexual, courtship, pre-copulatory,	Courtship [‡]	predominantly during breeding period	specific (<i>i.e.</i> , display is performed by and/or directed to a specific sex)
Wetmore ^{76,77}	nuptial, pairing, mating, pair forming ... [†]	Reproduction [‡]		
Sick ³⁵		<i>Cerimônias pré-nupciais, Reprodução</i> [‡]		
Bent ⁶³⁻⁷²		Courtship [‡]		
Lislevand et al. ⁷⁸	-	Display	-	-
<i>Internet Bird Collection</i>	-	-	-	intersexual (male to female or female to

male)[§]

280 *Function of the display as interpreted by the author. For instance, in the passage “I
281 saw the courtship flight song of the male [horned lark]”⁶³ (p. 327), the display’s explicit
282 function is “courtship” and it was thus taken to be sexual. In the passage “[t]he ‘up-
283 fluffing’ behavior of the [Yucatan] jays works as a signal of appeasement”⁷⁹, on the
284 other hand, display’s explicit function is “appeasement”. This display was not
285 considered to be sexual and thus is irrelevant for data collection purposes.

286 †Ambiguous: same functions but preceded by *apparently, may or may not be, probably ...*

287 ‡Ambiguous: other sections, but sexual function could not be ruled out

288 §Ambiguous: intraspecific, regardless of sex

289

290 *Habitat data*

291 We collected data about habitat structure (for all passerines) and foraging stratum (for
292 forest passerines only) from Parker et al.⁸⁰ and del Hoyo et al.³¹. The question *do*
293 *individuals occupy primarily open or forest habitats?* was answered *open* (1) if first
294 (primary) habitat listed for the species in Parker et al.⁸⁰ was of type *non-forest* or *aquatic*,
295 and *forest* (0) if primary habitat was of type *forest* (see Supplementary Methods for
296 which habitats are classified as non-forest, aquatic and forest by Parker et al.⁸⁰). We
297 were able to collect habitat data for 2,160 species (88.4% of the species in our initial
298 sample set) from this source, which only lists birds breeding in the Neotropical region
299 (*i.e.*, “from northern Mexico to the southern tip of Argentina, including the West
300 Indies”⁸⁰, p. 120). For the remaining species, we assigned the first habitat listed in
301 section *Habitat* in del Hoyo et al.³¹ to the closest habitat category used by Parker et al.⁸⁰
302 and determined whether it was a non-forest-, aquatic- or forest-type habitat. In a
303 random sample of 100 species evaluated from both sources, agreement as to openness
304 of habitat was very high (97%; posterior mean correlation = 0.97; 95% CI: 0.88 to 1). We
305 were able to determine primary habitat for 2,436 species (99.8% of the initial sample
306 set).

307 We searched for information about stratum only for species that occupy forest-
308 type primary habitats ($N = 1,864$ species). The question *do individuals forage exclusively*
309 *in canopy stratum?* was answered *yes* (1) if all foraging strata listed for the species in
310 Parker et al. (1996) were either *canopy* or *aerial*, and *no* (0) if any other forest stratum
311 was listed. For species not listed in Parker et al. (1996), we referred to del Hoyo et al.
312 (2018) using the same criteria (but considering *subcanopy* as *canopy*). We were able to
313 determine foraging stratum for 1,709 species (91.7% of forest species). Stratum data
314 were only used in the analysis whose results are shown in the Supplementary
315 Information.

316

317 *Phylogeny*

318 We used species-level Passeriformes trees based on the Hackett backbone from Jetz et
319 al.³⁷ (downloaded from <http://birdtree.org> on 18 March 2018). In each analysis, we
320 pruned trees to match the corresponding species for which we had complete data (*i.e.*,
321 species with missing data were dropped from the trees). Of the 469 species that were
322 included in the main analyses, 415 (88.5%) have had their phylogenetic position
323 determined based on genetic data³⁷ (Supplementary Data).

324

325 *Phylogenetic logistic regressions*

326 We used phylogenetic logistic regressions³⁸ to test for the influence of primary habitat
327 structure on the probability of passerines exhibiting aerial display ($N = 469$ species),
328 and to test for the influence of foraging stratum on the probability of forest passerines
329 exhibiting aerial display ($N = 235$ species; Supplementary Results). In the first analysis,
330 we compared a model with no predictor variable to one including habitat structure as
331 a categorical predictor. We fitted each model using the function `phyloglm` from
332 package `phylolm`⁸¹ (version 2.5) in R⁸² (version 3.4.3). To account for phylogenetic

333 uncertainty^{83,84}, we fitted each model iteratively using a sample of 1,000 different trees
334 from Jetz et al.³⁷, totalling 2,000 models. We fitted null models manually, and models
335 predicted by habitat using the package sensiPhy⁸⁵ (version 0.8.1). From each of the
336 2,000 models, we extracted Akaike information criterion (AIC) value as well as the
337 coefficients' estimates and p -values. The model with the lowest AIC was selected in
338 each iteration, as long as the competing model's Δ AIC was greater than 2. Estimates
339 were considered statistically clear if $p \leq 0.05$ ⁸⁶. According to our hypothesis, we
340 expected that the model containing habitat structure as a predictor would be selected
341 in most iterations, with a positive slope estimate.

342

343 *Correlated evolution of discrete characters*

344 A different approach to test the hypothesis that aerial displays are more likely to
345 evolve in open-habitat passerines than forest ones was to use Pagel's³⁹ method of
346 detecting correlated evolution between characters. We performed this analysis using
347 the Discrete module in BayesTraits V3.0.1⁴⁰ under a maximum-likelihood (ML)
348 approach. In order to test our hypothesis with this method, we had to ultimately assess
349 whether the evolutionary rate of gain of aerial displays is higher in species that live in
350 open habitats than in species that occupy forests. But a few steps precede this
351 assessment, and we will get to them below.

352 Pagel's method is based on continuous-time Markov chains with finite state
353 space (Mk model), which calculates the probability that a trait will change from state i
354 to state j over a very (infinitesimally) short time interval^{39,87}. This probability is called
355 instantaneous transition rate and is represented by the parameter q_{ij} . In this study, we
356 have two binary characters that, combined, result in four possible states a species may
357 assume: forest without aerial display, open habitat without aerial display, forest with
358 aerial display, and open habitat with aerial display. Let us call these states 1 to 4,

359 respectively — because it is the order in which they appear in Figure 2. In this figure,
360 each arrow corresponds to a parameter q . By looking at q_{12} , for example, we are looking
361 at the probability that a species that does not exhibit aerial display transitions from
362 forest to open habitat. Note that there are eight possible parameters (eight arrows)
363 because the diagonals are assumed to be zero; since we are dealing with a very short
364 time interval, it is assumed that both traits cannot change at the same time.

365 Pagel³⁹ suggests four biologically plausible models by which two characters can
366 evolve. If the characters evolve independently (*i.e.*, independent model), the transition
367 rates in one character do not depend on the state of the other character. In this model,
368 the transition from forest to open habitat, for example, is assumed to be the same
369 regardless of whether the species does or does not exhibit aerial display ($q_{24} = q_{12}$).
370 Likewise, the transition from presence to absence of aerial display is the same
371 regardless of the species' preference of habitat structure ($q_{31} = q_{43}$). The same holds true
372 for the remaining two pairs of parameters ($q_{13} = q_{34}$; $q_{42} = q_{21}$). The independent model is
373 the most parsimonious one, because it has only four free parameters (with the other
374 four restricted to have the same value as the free ones). Alternatively, if the characters
375 evolve in a correlated manner (*i.e.*, correlated model), all eight parameters are free to
376 vary: gain of aerial display depends on habitat ($q_{12} \neq q_{24}$), transition from forest to open
377 habitat depends on presence of aerial display ($q_{13} \neq q_{34}$), and so on. This is the least
378 parsimonious model, with eight free parameters. In between the independent and
379 correlated models, Pagel suggests that one character may influence the evolution of
380 another, but not the other way around. Thus, if only presence/absence of aerial display
381 influences preference for habitat structure (*i.e.*, display-dependent model), the
382 transition rates between habitats should be different depending on whether the species
383 exhibits or not aerial display ($q_{12} \neq q_{34}$; $q_{21} \neq q_{43}$), but gain and loss of aerial display are
384 assumed to be the same regardless of the habitat ($q_{13} = q_{24}$; $q_{31} = q_{42}$). Analogously, in the

385 habitat-dependent model, gain and loss of aerial display are different according to the
386 habitat ($q_{13} \neq q_{24}$; $q_{31} \neq q_{42}$), but transitions between habitats are the same regardless of
387 aerial display presence ($q_{12} \neq q_{34}$; $q_{21} \neq q_{43}$). Both habitat-dependent and display-
388 dependent model have six parameters each.

389 We extracted the AIC value of each model using the following equation, where
390 k is the number of parameters (*i.e.*, number of free qs) and \hat{L} is the maximum
391 likelihood:

$$392 \quad \text{AIC} = 2k - 2 \ln(\hat{L})$$

393 We also calculated the Akaike weights (w_i) of each model to assess the weight
394 of evidence in its favour relative to all the other models in the set^{41,88}. Next, we used a
395 model-averaging approach to estimate the parameter values. For a given parameter q ,
396 we did that by weighting the ML estimate in each of the four models (\hat{q}_i) by the
397 model's w_i , resulting in the model-averaged ML estimate $\hat{q}^{41,89}$:

$$398 \quad \hat{q} = \sum_{i=1}^4 w_i \hat{q}_i$$

399 We decided to use a model-averaging procedure because it offers advantages
400 such as basing inference not just on the one model estimated to be the best, but on all *a*
401 *priori* models⁸⁹, and avoiding the need for subjective thresholds to choose which model
402 is the best⁹⁰. After performing model averaging, we were then able to properly test our
403 hypothesis by comparing the model-averaged ML estimate of the rate of gain of aerial
404 display in open habitats (q_{24}) and forests (q_{13}), predicting that $q_{24} > q_{13}$.

405 All steps described above were repeated for each tree in the 1,000-tree sample
406 from Jetz et al.³⁷ to account for phylogenetic uncertainty, and the rates shown by the
407 arrows in Figure 2 are the median model-averaged ML estimate for each transition
408 rate, multiplied by 10^2 , across the 1,000 trees.

409 **Data availability**

410 All of the R code and data used in our analyses will be made available on Dryad upon
411 acceptance of the paper.

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634 **Competing interests**

635 The authors declare no competing interests.