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Convergent evolution in social swallows (Aves: Hirundinidae)

Running Title: Social swallows are morphologically convergent

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Data archiving: Social and morphological data and R code utilized for data analysis have been submitted as supplementary material associated with this manuscript.

Abstract: Behavioral shifts can initiate morphological evolution by pushing lineages into new adaptive zones. This has primarily been examined in ecological behaviors, such as foraging, but social behaviors may also alter morphology. Swallows and martins (Hirundinidae) are aerial insectivores that exhibit a

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30 range of social behaviors, from solitary to colonial breeding and foraging. Using a well-resolved
31 phylogenetic tree and a database of social behaviors and morphology we ask how shifts from solitary to
32 social breeding and foraging have affected morphological evolution in the Hirundinidae. Using a
33 threshold model of discrete state evolution, we find that shifts in both feeding and breeding social
34 behavior are common across the phylogeny of swallows. Solitary swallows have highly variable
35 morphology, while social swallows show much less absolute variance in all morphological traits.
36 Metrics of convergence based on both the trajectory of social lineages' through morphospace and the
37 overall morphological distance between social species scaled by their phylogenetic distance indicate
38 strong convergence in social swallows, especially socially foraging swallows. Smaller physical traits
39 generally observed in social species suggest that social species benefit from a distinctive flight style,
40 likely increasing maneuverability and foraging success and reducing in-flight collisions within large
41 flocks. These results highlight the importance of sociality in species evolution, a link that had
42 previously been examined only in eusocial insects and primates.

43
44 **Keywords:** coloniality, convergent evolution, morphology, sociality

46 **Introduction**

47 Animal morphology and behavior are inextricably linked, with particular morphologies
48 permitting particular behaviors, and behavioral innovation producing novel selective pressures on
49 relevant morphologies. For example, the resonant vocalizations of sandhill cranes (*Grus canadensis*)
50 require the extension of the trachea into the sternum (Johnsgard 1983), and the territorial displays of
51 red-winged blackbirds (*Agelaius phoeniceus*) are less effective against intruders without the male's
52 bright red wing epaulettes (Yasukawa and Sercy 1995). Changes in behavior have long been implicated
53 in initiating changes in morphological traits by affecting how species interact with their environment
54 and by altering selective pressures (Duckworth 2008; Lapiedra et al. 2013). A number of studies have
55 examined how behaviors associated with ecological differences between species, such as preference for
56 certain habitats, direct morphological evolution (e.g., Miles and Ricklefs 1984; Losos 1990; Douglas
57 and Matthews 1992; Streelman et al. 2002; Desrochers 2010).

58
59 Social behavior should play a similar role in influencing morphological evolution, with species
60 changing in accordance with the new physical demands involved in performing social or group
61 behaviors; but social behavior's influence has been rarely studied in non-extinct species. For instance,

62 ecological influences such as the cluttered foraging habitat of bats have been shown to influence wing
63 morphology (Sauders and Barclay 1992; Kalcounis and Brigham 1995), but a similar pressure from
64 social behavior to prevent collisions in large social roosts could produce repeated convergence of wing
65 morphology. Social behavior has been linked to the evolution of morphology in eusocial insects, with
66 diversity in number of castes and caste morphology linked to colony size and complexity (Bourke
67 1999; Fjerdingstad and Crozier 2006). In mammals, the relationship between brain morphology and
68 social behavior has been well studied (e.g., Dunbar 1995; Shultz and Dunbar 2007, 2010; Noonan et al.
69 2014), but little work has been done to link sociality to morphological evolution more broadly in
70 vertebrates.

71
72 To better understand the role of social behavior in influencing morphological evolution, we
73 compared the evolution of morphological features important to flight and foraging to the evolution of
74 social behaviors in the socially diverse bird clade the Hirundinidae (swallows and martins, see Fig. 1
75 for an image of one member of the Hirundinidae family). The Hirundinidae consist of 84 species
76 distributed worldwide, which have a long history of field studies focused on social behaviors, foraging
77 strategies and general natural history (Beecher et al. 1981; Møller 1987; Brown 1988; Brown and
78 Brown 1996, 1998, 2000, 2011, 2013, 2014, 2015; Turner and Rose 1989; Turner 2004; Sheldon et al.
79 2005; Roche et al. 2011; Brown et al. 2013; Brown et al. 2016). All species are obligate aerial
80 insectivores (Turner and Rose 1989; Turner 2004), a foraging strategy that requires agile, acrobatic
81 flight. However, they exhibit great diversity in their degree of sociality (e.g., solitary to colonial
82 breeding, solitary to group foraging). Breeding group sizes can range from a single pair to as many as
83 6000 pairs (Turner and Rose 1989; Turner 2004; Brown et al. 2013). Foraging group sizes range from
84 individuals and pairs foraging in isolation to flocks of hundreds of individuals foraging in close
85 proximity (Ricklefs 1971; Brown and Brown 1996; Santema et al. 2009; Graves 2013). Group foragers
86 most often exploit swarming or aggregating species of insects, including mass emergences, mating
87 swarms, insects caught in local convection currents or sheltering in the lee side of hills under inclement
88 conditions (Brown and Brown 1996). Insects utilized by group foragers are typically smaller than those
89 consumed by non-social foragers (Bryant and Turner 1982; Turner 1982; Quinney and Ankney 1985;
90 Brown and Brown 1996).

91
92 Using published behavioral and ecological data from 40 sources (see Table A2 in Appendix A),
93 measurements of 525 museum specimens, and a phylogeny from Sheldon et al. (2005) encompassing
94 75 of the 84 swallow species, we asked how breeding and foraging social behavior is correlated with

95 the evolution of external morphology. We define sociality as intraspecific interactions that occur during
96 breeding and foraging. In the raw data shown in Fig.1, a pattern of reduced morphological diversity in
97 social species is apparent, with solitary species showing a wider range of variation across all measured
98 traits. This pattern has four potential explanations: 1: it could be a spurious result of a small number of
99 social species; 2: it could be a spurious result from a single ancestral swallow that became social, and
100 all subsequent descendants inherited similar morphology (phylogenetic autocorrelation); 3: social
101 species could have an additional constraint, such as occurring only in a specific habitat, that selects for
102 a particular morphology; 4: social habits may exert a direct selection on morphology by increasing
103 competition between individuals in a social group for the same resources (including flight space or
104 aerodynamic requirements for maneuverability) promoting morphological convergence.

105

106 In this study, we explore these different explanations and attempt to determine which is most
107 likely to explain the observed patterns. We use a liability threshold model of social evolution to
108 understand the pattern of social evolution along the swallow phylogeny (Felsenstein 2012; Revell
109 2014). Models of discrete character evolution that rely on a transition matrix assume a consistent rate
110 of evolution across the whole tree, making similarly-sized clades with different levels of heterogeneity
111 problematic. After reconstructing the evolution of social evolution, we used various metrics of
112 convergence (Arbuckle et al. 2014; Stayton 2015) to test whether the social species converged on each
113 other, and quantified the strength of that convergence.

114

115 **Materials and Methods**

116 **Morphological Measurements.** We measured 6 external morphological traits on 525 museum
117 specimens (skins) from 73 species of swallows and martins (data deposited on Dryad and available in
118 Table A1 in Appendix A). These species represent 19 of the 21 genera in the Hirundinidae, excluding
119 only *Haplochelidon* and *Alopochelidon*, both of which contain only one species (Dickinson 2003;
120 Clements et al. 2014). To balance time spent measuring a single species against sample size, we
121 measured five males and five females of each species whenever possible. For species without five
122 males and females in the museum collections, we measured all available specimens. For seven species,
123 we were only able to measure one specimen (see Dryad data file). To account for how specimens
124 shrink over time, are prepared using different techniques, and the fact that plumage can vary by season,
125 we measured specimens that were of approximately the same age, collected at the same time of year
126 and made by the same preparator, when possible. Specimens used in our analyses are housed in the

127 collections of the Field Museum of Natural History (Chicago, IL), the Smithsonian Institution
128 (Washington, DC), and the Louisiana State Museum of Natural Science (Baton Rouge, LA).

129

130 The following traits were measured for all specimens: wing length, depth of the tail fork, outer
131 tail feather length, tarsus length, bill length, and bill width. For all specimens, the length of each
132 unflattened, closed wing (from the anterior most part of the wrist joint to the tip of the outermost
133 primary) was measured to the nearest 1 mm with a stoppered wing ruler; the length of the middle tail
134 feather and the two outermost tail feathers (from the emergence from the skin to the distal most point)
135 were measured to the nearest 1 mm with a ruler; the length of each tarsus (from the proximate end of
136 the tarso-metatarsus to the hallux) was measured to the nearest 0.1 mm with calipers; and the length
137 and width of the exposed bill (length from the proximate end of the exposed bill to the tip along the
138 ridge of the upper mandible and width of the exposed mandibles at the level of the nostrils) was
139 measured to the nearest 0.1 mm with calipers. While many studies examining wing morphology
140 include Kipp's distance (distance between longest primary feather and the first secondary feather when
141 the wing is closed; Kipp 1942; Dawideit et al. 2009), we were unable to take this measurement because
142 of the condition or preparation of the specimens used. The outermost primary feather length has been
143 used in other studies of morphology and wing evolution in swallows and serves as a practical proxy
144 (Brown and Brown 1996; Price et al. 2000; Brown and Brown 2011; Brown and Brown 2013). One
145 person took all morphometric measurements (MBB), and thus no corrections to the data for multiple
146 measurers were necessary. Repeatability estimates for these same body size measurements (cliff
147 swallow, *Petrochelidon pyrrhonota*, Fig 1.), made by MBB were all statistically significant ($p < 0.001$;
148 see Brown and Brown 1998). Measurements were taken on both left and right sides of each specimen
149 (when appropriate) and averaged. We evaluated the tail shape reflected in the depth of the tail fork by
150 subtracting the middle tail length from the mean outer tail length. All categories (wing, outer tail, depth
151 of tail fork, tarsus, bill length, and bill width) were averaged across all individuals (male and female)
152 measured for each species. For all analyses described below, trait values are all relative to the length of
153 the tarsus to control for variation in body size.

154

155

156 **Behavioral Scoring.** We used two measures of sociality—breeding behavior and foraging behavior.
157 We chose two metrics as these forms of sociality may result in differing selective pressures and while
158 most socially breeding species forage socially, some solitary breeding species also forage socially. For
159 breeding behavior, we performed a primary literature search to find the maximum reported breeding

160 group size for every species with sufficient behavioral data recorded (see Table A2 and associated
161 references in Appendix A for all citations). All species with appropriate data were then categorized as
162 either social or solitary. Social species are those species that have been documented nesting in groups
163 of five or more pairs. The two species documented as forming ‘colonies’ of two to five pairs (*Progne*
164 *sinaloae* and *Notiochelidon murina*) utilize existing cavities rather than constructing them and are only
165 found in groups larger than pairs when cavities are spaced near one another. They do not appear to
166 exhibit any social cohesion and we therefore classified these species as solitary.

167
168 As for breeding behavior, foraging behavior was determined based on a primary literature
169 search. Foraging behavior was divided into two categories, pairs and groups. The pair foraging
170 category was defined as species that have been observed primarily to forage solitarily or as breeding
171 pairs only. Pair foraging represents the “solitary” category for foraging behavior, but is defined as pair
172 because most solitary species will forage with their mate over the course of the breeding season (Turner
173 2004). The group foraging category was defined as species observed to forage in groups beyond the
174 breeding pair. Some species were placed in the pairs or groups categories based on descriptions of
175 behavior if specific foraging group size counts were lacking. One species, *Notiochelidon flavipes*, had
176 data on foraging behavior and was included in the foraging data set, but lacked data on breeding
177 behavior.

178
179 As engaging in one social behavior may relate to the propensity to engage in another, we tested
180 whether foraging behavior and breeding behavior are correlated. Analyses were carried out over 1000
181 simulations testing for any effect (x is dependent on y or y is dependent on x) in Mesquite 3.02
182 (Maddison and Maddison 2015) using the *correl* package. The evolution of foraging behavior and
183 breeding behavior is correlated ($p=0.006$, Pagel’s correlation test; Pagel 1994). This is unsurprising
184 given that most social breeding species also forage socially (Table 1). Despite this correlation, we
185 chose to analyze these traits separately because many solitary breeding species also forage socially.
186 Additionally, there is much more variation in the manifestation of social breeding, with colony sizes
187 varying from a single pair to 6000 pairs (Turner 2004, Brown et al. 2013), so the selective pressures of
188 foraging socially and breeding socially may be quite different.

189
190 **Statistical analyses.** We completed descriptive summary statistics for all morphological traits
191 separated by behavioral category. The mean and standard deviation (SD) for each trait were calculated
192 for species that breed solitarily or socially and forage in pairs or groups. SD was calculated rather than

193 standard error (SE) to illustrate the difference in the variability of each morphological trait in social and
194 non-social species. We performed *t*-tests (using phylANOVA from phytools; Revell 2011) between
195 solitary and social categories and between pair and group foraging categories for each morphological
196 trait to determine if the mean trait values were significantly different between solitary and social
197 species. We used the multiple testing correction of Holm (1979) to account for the many separate tests.

198
199 **Phylogenetic analyses and model testing.** Our phylogenetic analyses utilized the molecular
200 phylogeny presented in Sheldon et al. (2005). The Sheldon et al. phylogeny contains sequence data for
201 75 of the 84 currently recognized species in the Hirundinidae (Dickinson 2003; Clements et al. 2014).
202 Of these 75 species, 72 are used in our analyses of breeding behavior and 73 are used in our analyses of
203 foraging behavior. *Pseudochelidon sirintarae*, *Haplochelidon andecola*, and *Progne murphyi* were
204 excluded from all analyses due to lack of morphological data. *Notiochelidon flavipes* was excluded
205 from analyses of breeding behavior due of lack of data, but was included in foraging behavior analyses.
206 To prevent inflation of the data at the tree tips, we excluded the following subspecies from all analyses:
207 *Psolidoprocne pristopectera petiti*, *P. p. orientalis*, and *Hirundo rustica erythrogaster*. Instead, these
208 species were represented in the analyses by the subspecies *P. p. holomelas* and *H. r. rustica*. These
209 subspecies were chosen over the others because they were represented by more complete genetic
210 sampling. The Sheldon et al. (2005) phylogeny included four outgroup species, which we excluded
211 because they were not swallow species.

212
213 To illustrate how morphology clusters with social behavior, we generated phylomorphospaces
214 for the group size of breeding colonies and the raw morphological measurements (Sidlauskas 2008).
215 Scatter plots were generated only for breeding behavior because breeding group size was more
216 accurately available in the literature than foraging group size; foraging group size is often referenced
217 vaguely in primary literature (e.g., large group, small group). Both the phylomorphospaces and scatter
218 plots are raw data not subject to any direct analysis, and as such they should be treated as exploratory
219 analyses depicting the first-order relationship of sociality and morphology.

220
221 Convergence is a difficult aspect of evolution to measure (Stayton 2015). We used two different
222 methods to first test for, and then quantify the strength of, convergence. First, we used four indices
223 (C1-C4) that quantify how social lineages move through phenotypic space (Stayton 2015). These
224 indices use ancestral state reconstruction to look at the extent to which species have evolved greater
225 similarity to one another. By comparing the distance between two tips relative to their distance at the

226 point in the past where the two lineages were maximally dissimilar (C1), it is possible to test if
227 particular lineages are moving towards one another in phenotypic space. Likewise, the raw value of the
228 difference between the maximum and extant distance between the two lineages (C2) can be scaled by
229 either the total evolution (sum of squared ancestor-to-descendant changes) between the two lineages
230 (C3) or the total evolution in the whole clade (C4). These metrics rely on ancestral state reconstruction
231 of the various characters; however, these indices are the only reliable way to detect incomplete
232 convergence in multidimensional space. We reconstructed ancestral states using the Bayesian
233 implementation of the threshold model described by Revell (2014) with 2,000,000 generations
234 sampling every 2,000 generations, and discarding the first 10% as burn in. The threshold model is more
235 appropriate as the liability can be interpreted as an unobserved continuous trait (such as blood hormone
236 levels) and allows for different clades to have variable levels of liability. For instance, *Hirundo* includes
237 both social and solitary species while *Petrochelidon* is exclusively social, which would bias rate matrix
238 approaches to ancestral state reconstruction. Significance was tested by simulating trait evolution 1000
239 times along the phylogeny and determining what fraction of random-trait evolution simulations show
240 higher levels than the observed data.

241
242 Another metric of convergence, which does not rely on ancestral state reconstruction, is the
243 Wheatsheaf index (Arbuckle et al. 2014). The Wheatsheaf index compares the mean distance in
244 phenotypic space between social species to the overall average distance between all pairs of species,
245 and scales those comparisons by the phylogenetic variance-covariance matrix. Unlike Stayton's (2015)
246 indices, the Wheatsheaf index cannot test for incomplete convergence, nor does it test for the presence
247 of convergence per se. Rather, it quantifies the strength of convergence among taxa and, by permuting
248 the tip data, tests whether or not that strength is significant relative to the overall evolution of the clade.
249 One major advantage of the Wheatsheaf index is that it makes no assumptions about the ancestral
250 states; it is simply a phylogenetically-corrected statistic of distances between taxa.

251
252 Finally, we also used the package *l1ou*, a model-based approach to detecting convergence which
253 employs LASSO (least absolute shrinkage and selector operator) to determine the optimal number of
254 selective regimes in a phylogeny (Khabbazian et al. 2016). *l1ou* paints a phylogeny with different
255 Ornstein-Uhlenbeck models (Hansen 1997; Butler et al. 2004; Beaulieu et al. 2012) to determine how
256 many different selection regimes are needed to explain the data, and then tries to collapse those regimes
257 together. Convergence is indicated by either identical (collapsed) or very similar sets of OU parameters
258 in distantly related taxa. This method requires no prespecification of taxa nor the number or location of

259 rate shifts. All inferred heterogeneity and the positions of transitions are automatically detected.
260 However, this approach is fully model based, and subject to all the perils of OU models in general (for
261 example, see Cooper et al. 2016), and only allows for shifts in the theta value. In our study, it is
262 primarily useful in demonstrating non-homogenous evolutionary dynamics.

263

264 All calculations, graphs, and simulations were completed in R 3.1.0 (R Core Team 2014), using
265 functions from the packages “vegan”, “ape”, “phytools”, “l1ou”, “MASS”, “msm”, and their
266 dependencies (Paradis et al. 2004; Jackson 2011; Revell 2011; Oksanen et al. 2013; Beaulieu and
267 O’Meara 2014; Khabbazian et al. 2016). All code, data, and model fitting outputs are archived at Dryad
268 (XXXX).

269

270 **Results**

271 **Descriptive statistics.** Most morphological traits, whether in solitary or social categories of breeding
272 and foraging behavior, have similar mean values (Table 1). For breeding behavior, only the mean bill
273 length and width are significantly smaller in social than solitary species (two-tailed *t*-test, Table 1). For
274 foraging behavior 4 morphological traits (outer tail length, depth of tail fork, tarsus length and bill
275 width) are significantly smaller in group foragers compared to solitary species (two-tailed *t*-test, Table
276 1). While not all morphological traits differ between solitary and social species, the mean value of the
277 traits of social breeders and foragers generally have smaller standard deviations than that of non-social
278 species (3 of 6 traits for breeding behavior and 5 of 6 for foraging behavior; Table 1).

279 The low external morphological variation in social species is illustrated by the scatter plots of
280 maximum breeding group size (Fig. 2). Species that exhibit solitary behavior fill a broader
281 morphological space than species that exhibit social behavior; the small morphological space filled by
282 socially breeding species remains the same despite variation in group size.

283

284 **Repeated evolution of social behaviors.** Of the 72 species that are included in our analyses of
285 breeding behavior, 33 species were categorized as solitary and 49 were categorized as social. Of the 73
286 species included in our foraging dataset, there are 20 species that forage either solitarily or in pairs
287 while 53 forage in large groups. Transitions in behavior were common, but unevenly distributed across
288 the phylogeny. Some genera, such as *Hirundo* and *Progne* have multiple transitions to and from social
289 behavior while older genera like *Petrochelidon* show no heterogeneity at all. The ancestral swallow is
290 well-supported as a social breeder and forager in our analyses based on the threshold model.

291

292 **Testing for and quantifying convergence.** Both socially foraging and breeding swallow species
293 converged significantly according to the indices of Stayton (2015). Social swallows show 22%
294 convergence in the morphological traits measured, which represents about 10% of the overall
295 phenotypic evolution of the social species and 1% of morphological evolution in all swallows. This
296 amount of convergence was significant in both foraging ($p = 0.007$) and breeding ($p = 0.002$) based on
297 1000 Brownian Motion simulations. Likewise, the Wheatsheaf index shows strong convergence in both
298 social breeders and foragers, although only the strength of convergence in social foragers is significant
299 ($p < 0.01$; Fig. 3). Hou analysis (Khabbazian et al. 2016) found evidence for 13 shifts in breeding
300 behavior (Fig. 4) and 11 shifts in foraging behavior (Fig. 5). Many of these shifts in evolutionary
301 regimes occurred on branches where transitions in social behavior occurred. Hou only allows for
302 changes in the trait optimum, making it difficult to compare directly with other methods. However, the
303 results clearly indicate heterogeneity in swallow phenotypic evolution.

304

305 **Discussion**

306 Sociality in the Hirundinidae appears to be associated with changes in morphology, with social
307 species exhibiting smaller, more constrained morphological traits than their non-social relatives (Fig.
308 2). This pattern can be explained in four ways. Either it is the result of 1) a small sample size, 2)
309 phylogenetic autocorrelation in which one ancestral swallow became social and its descendants
310 inherited a similar morphology, 3) constraint on social species from something other than behavior,
311 such as habitat, or 4) direct selection on morphology driven by sociality, by increasing competition for
312 shared resources and promoting convergence. Social breeding and social foraging have been acquired
313 and lost repeatedly in the Hirundinidae with significant consequences for the evolution of external
314 morphology. The repeated shifts between social and non-social behavior in the Hirundinidae reduce
315 support for the first two explanations, as convergence upon morphology had to have occurred multiple
316 times, and could not have come from a single common ancestor. The patterns of lower variation and
317 higher convergence in social, relative to solitary, swallows were observed in the raw data (Fig. 2) and
318 supported by a variety of analyses. Comparison of the evolutionary trajectories of social and solitary
319 lineages strongly support convergence in social species, as does a simple, phylogenetically-corrected
320 calculation of how clumped social species are in morphospace.

321

322 All swallows are aerial insectivores suggesting all species must be near a similar morphological

323 optimum to allow for aerial foraging (Turner 2004). Convergence occurs in both socially breeding and
324 foraging species, although the convergence is stronger in socially foraging species. Solitarily foraging
325 species typically consume larger, more solitary insect prey than do social foraging species, which often
326 feed on mass insect emergences (Bryant and Turner 1982; Turner 1982; Quinney and Ankney 1985;
327 Brown and Brown 1996; Chişamera and Manole 2005; Fernandes et al. 2007; Boukhemza-Zemmouri
328 et al. 2013; Orłowski and Karg 2013; MBB, pers. obs.). While this difference in prey types may
329 suggest ecology to be an important driver of morphological changes, swallows may only be able to
330 specialize on small ephemeral insects when sharing information within a flock, suggesting a
331 combination of social and ecological behaviors alter the optimal morphologies in different swallows.
332 Avoiding collisions as multiple individuals feed on the same emergent insect swarm may necessitate a
333 particular acrobatic morphology, and so may explain our results.

334

335 Both social foraging and social breeding require agile flight. Species that require aerodynamic
336 maneuverability tend to have proportionately shorter tails and wings, which provide high lift to drag
337 ratios, whereas species that require less agile flight typically have longer tails (Thomas and Balmford
338 1995; Brown and Brown 2013). Wing length and outer tail length are significantly shorter in group
339 foraging species than in pair foraging species. Depth of tail fork is also smaller in group foraging
340 species than in pair foraging species, however this result is marginally significant. The shorter outer tail
341 length and shallower depth of tail fork result in a more square-shaped tail in group foraging species.
342 These patterns hold for breeding behavior but are not statistically significant. Separate from social
343 foraging, agile flight in social breeders may be advantageous by reducing the likelihood of collisions at
344 colony sites where many birds are moving in and out of nests.

345

346 We also see significantly reduced bill length and width, resulting in relatively smaller bills, in
347 socially foraging species, a pattern which again holds for breeding behavior but which is not
348 statistically significant. The reasons for constraint in these traits may be two-fold. First, and most
349 importantly, bill size influences foraging success. All members of the Hirundinidae consume insects
350 they capture in flight. As noted above, insects consumed by non-social species (e.g., barn swallow,
351 *Hirundo rustica*) are typically larger in size compared to those consumed by social species (Bryant and
352 Turner 1982; Turner 1982; Quinney and Ankney 1985; Brown and Brown 1996; Chişamera and
353 Manole 2005; Fernandes et al. 2007; Boukhemza-Zemmouri et al. 2013; Orłowski and Karg 2013;
354 MBB, pers. obs.). Additionally, most of the insects consumed by social species are found in
355 aggregations (e.g., mating swarms, mass emergences, local convection currents) and birds foraging in

356 groups may be more able to locate and exploit them as a food resource. This has been shown in cliff
357 swallows (*Petrochelidon pyrrhonota*, Fig. 1), where colonies act as information centers and large
358 colonies facilitate tracking of ephemeral insects (Brown 1988). As social species specialize in foraging
359 on small ephemeral insects, large bills may be selected against. Second, bill size may influence the
360 construction of nest structures in social species (Winkler and Sheldon 1993). Species that form the
361 largest colonies (e.g., *Petrochelidon* sp.) all build mud retorts that require birds to collect, carry, and
362 adhere mud to form their nests using their beaks, and perhaps smaller bills influences transport and
363 application of mud. However, similar mud-type nests are found in a few of the solitary species (e.g.,
364 *Cecropis* sp., open mud cups, *Hirundo* sp.; Winkler and Sheldon 1993; Turner 2004), so we feel more
365 weight should be given to the foraging specialization hypothesis.

366
367 Our analyses suggest there is a consistent morphological ‘solution’ to being social in the
368 Hirundinidae, that is, social swallows have converged on only one morphological type. This is
369 supported by within species studies on cliff swallows which show no morphological difference
370 between swallows that occupy large colonies or small colonies, even though colony choice is heritable
371 for first year colony preference (Brown and Brown 1996, 2000; Roche et al. 2011). Aside from
372 Winkler and Sheldon’s (1993) study demonstrating a link between nest morphology and degree of
373 sociality in swallows, this is the first study illustrating a link between sociality and morphology in birds
374 of which we are aware.

375
376 We have shown that morphological evolution is associated with changes in social structure,
377 both in breeding and in foraging. As we are quantifying social foraging in addition to breeding, it is
378 obvious that the behaviors we observe are linked to ecological behaviors, such as the type and size of
379 insects preyed upon. However, it seems in swallows it is a change in social behavior that is changing
380 ecological behaviors, and both aspects of behavior influencing morphology. As such, social behavior is
381 the ultimate cause of these changes, however our data also suggest that the social behavior is the
382 proximate driver as well. While the evolution of certain nesting structures (e.g., mud retorts) either
383 facilitated or allowed the evolution of extremely large colonies (Winkler and Sheldon 1993), each nest
384 type is found in both solitary and social breeding species. Although foraging habitat (open or closed)
385 influences wing and tail morphology in other aerial insect feeders (e.g., bats; Kalcounis and Brigham
386 1995), swallows and martins are generally all found to forage in open habitat. This consistent foraging
387 preference for open habitats in swallows means that and we would not expect to see a shift towards
388 greater maneuverability unless driven by some other selective pressure. Finally, it is possible that

389 sexual selection may influence the evolution of morphologies observed in swallows. However, only
390 one species, *Hirundo smithii*, has extremely dimorphic morphological traits, with males exhibiting long
391 outer tail “streamers.” While sexual selection certainly results in dimorphic morphology in some
392 swallow species (Møller 1992; Møller and Birkhead 1994), males and female generally exhibit similar
393 morphologies and, except for in the case of *H. smithii*, we feel averaging morphological measurements
394 across sexes was sufficient to compensate for this variation.

395
396 We have shown that sociality produces morphological convergence in the Hirundinidae. In the
397 Hirundinidae, we see many transitions between solitary and social breeding behavior as well as
398 between pair and group foraging behavior, but the same morphology evolves every time a species
399 becomes social. This suggests that social behavior in the Hirundinidae is successful only within a single
400 morphological niche space. Further studies in taxa with both social and non-social behaviors may
401 inform whether the evolution of sociality consistently constrains morphological evolution or if, in some
402 cases, it promotes morphological diversity. More studies are necessary to understand the potential for
403 social behavior to alter the morphological evolutionary trajectory of species.

404

405 **Author Contributions**

406 All authors contributed to the design of the study. M.B.B. measured all the specimens. A.E.J. compiled
407 the behavioral data. A.E.J. and J.S.M. performed data analysis. All authors contributed to manuscript
408 writing.

409

410 **Data accessibility**

411 The datasets and code used and described in this article are archived at Dryad (XXXX).

412

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427

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606

607 **Figure 1.** A flock of cliff swallows (*Petrochelidon pyrrhonota*), one member of the Hirundinidae
608 family, collecting mud for nest building. Photo taken by Joel G. Jorgensen.

609

610 **Figure 2.** Phylomorphospaces of morphological trait values compared to maximum observed breeding
611 group size for A) outer tail length, B) depth of tail fork, C) wing length, D) tarsus length, E) bill length,
612 and F) bill width. All morphological values are scaled by tarsus except tarsus length.

613

614 **Figure 3.** Strength of convergence as measured by the Wheatsheaf index for social breeding (A) and
615 foraging (B) species. Histograms represent the distribution of the Wheatsheaf index for 1,000,000
616 randomizations of the data and the dashed lines show the value of the Wheatsheaf index for the

617 observed data.

618

619 **Figure 4.** Ancestral reconstruction of breeding behavior using the threshold model and evolutionary
620 regimes using I1ou. White icons denote solitary species, while black indicates social species, and pie
621 charts at each node show the posterior probability of each character state at that node. Edges are
622 colored by regime, and asterisks denote the location of regime shifts.

623

624 **Figure 5.** Ancestral reconstruction of foraging behavior using the threshold model and evolutionary
625 regimes using I1ou. As in Fig. 4, white icons denote solitary species, while black indicates social
626 species, and pie charts at each node show the posterior probability of each character state at that node.
627 Edges are colored by regime, and asterisks denote the location of regime shifts.

628

629 **Table 1.** Descriptive statistics for breeding and foraging behavior and results of phylogenetic t-test
630 based on 10,000 simulations for each trait in each social strategy. All measurements are in mm and all
631 p-values have been adjusted for multiple tests using the method of Holm (1979).

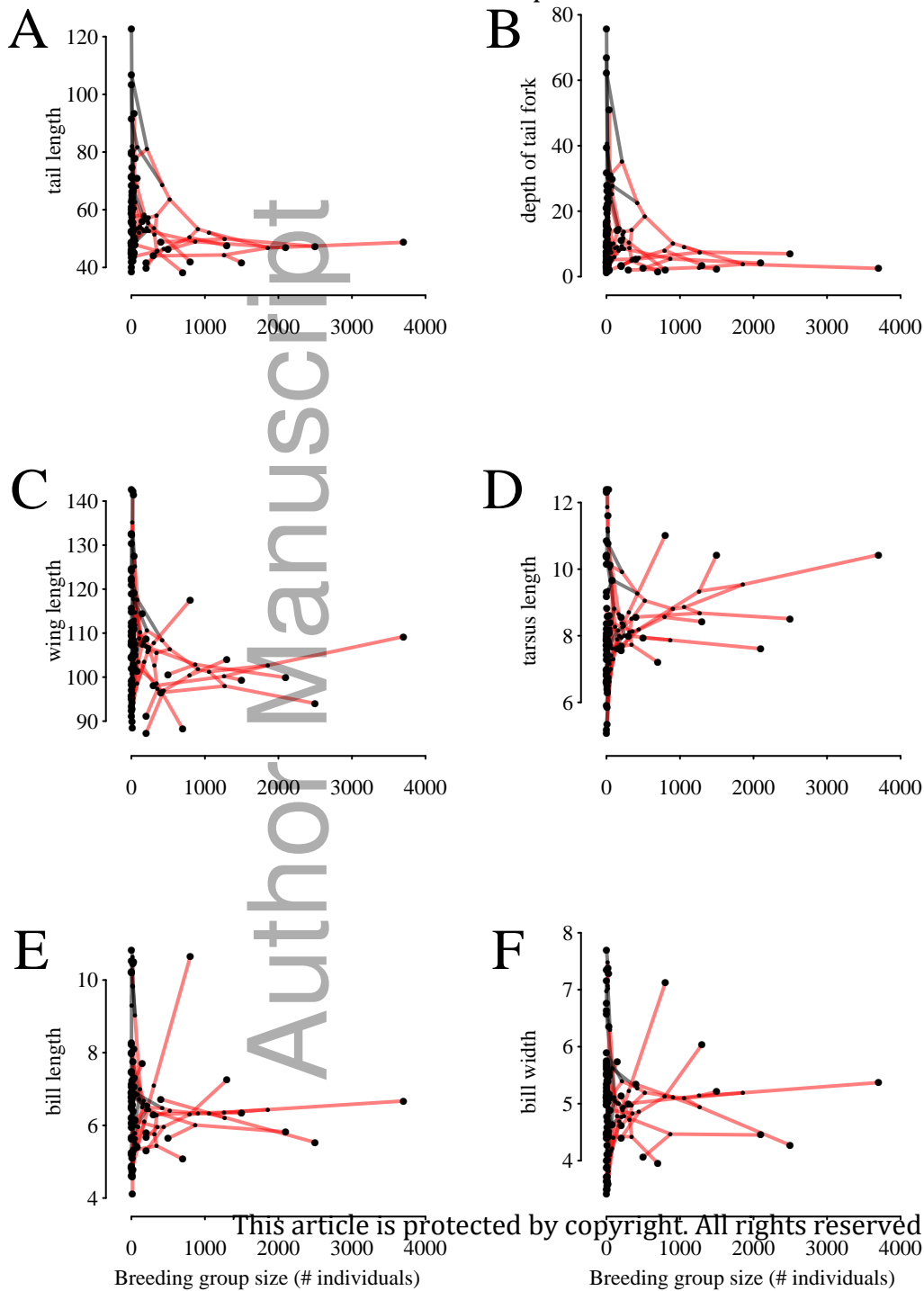
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	Breeding behavior					Foraging behavior				
	Solitary		Social		<i>p</i> -value	Pairs		Groups		<i>p</i> -value
	Mean	SD	Mean	SD		Mean	SD	Mean	SD	
Wing length	110.73	13.15	104.95	12.61	1	116.19	15.19	103.76	10.40	0.040
Outer tail length	61.25	21.70	55.00	12.74	1	68.82	24.44	53.29	11.67	0.047
Depth of tail fork	16.94	19.85	12.08	11.33	1	45.59	8.69	42.67	4.84	0.053
Tarsus length	8.16	1.77	8.11	1.65	1	8.98	1.88	7.77	1.48	0.053
Bill length	6.93	1.61	6.27	1.61	1	7.52	1.53	6.12	1.52	0.050
Bill width	5.23	1.09	4.80	1.06	1	5.68	0.90	4.65	1.02	0.040

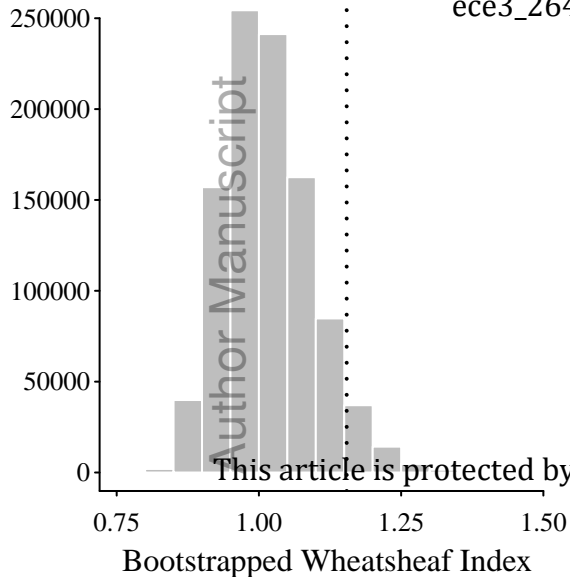
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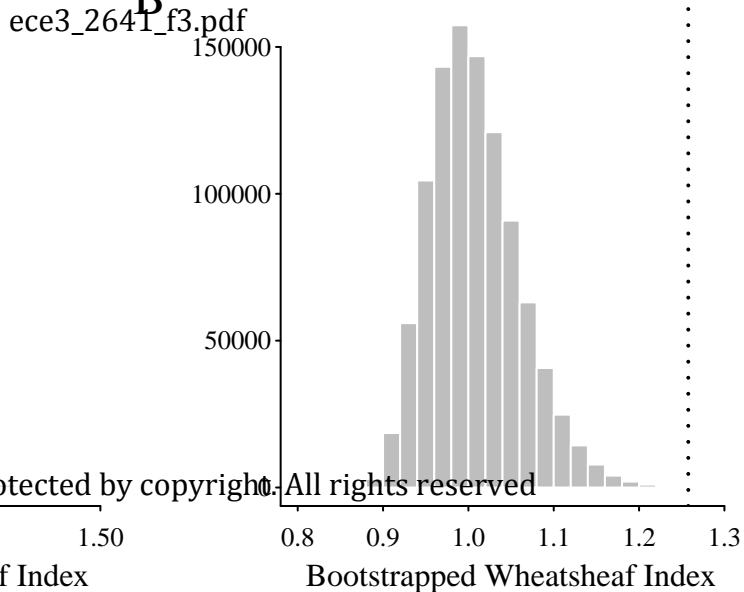
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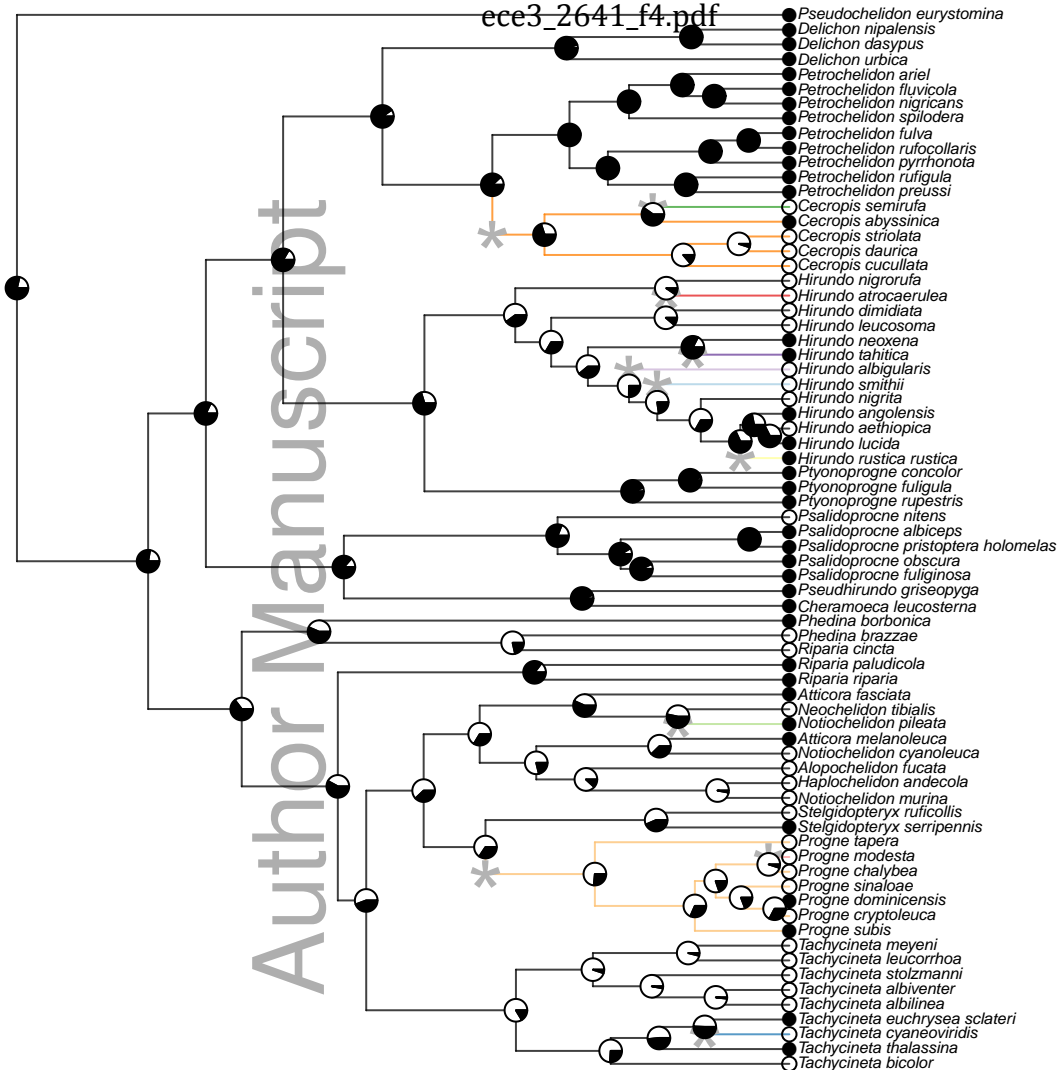


A



B





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