

1 The role of many-to-one mapping of vertebral form to function in Psittaciform
2 tripodal locomotion

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34 **Abstract (197/200 words)**

35 Parrots highlight the functional diversity of the avian neck by contributing to a range of behaviors,
36 including arboreal locomotion. The parrot neck is used alongside the beak and hindlimb to allow
37 them to successfully navigate arboreal habitats via tripodal locomotion. Whether specific
38 morphological characteristics of the neck enable this behavior are currently unknown. By combining
39 geometric morphometrics with phylogenetic comparative methods we investigate the factors
40 correlate with shape variation in the cervical vertebrae of parrots. We find that phylogeny, allometry,
41 integration, diet and tripodal locomotion all have a significant influence on the morphology of
42 psittaciform cervical vertebrae. However, the influence of diet and tripodal locomotion is weak, with
43 a high degree of morphospace overlap existing between dietary and neck use groups. Additionally,
44 we find no evidence of convergence in parrot neck morphology due to the incidence of tripodal
45 locomotion or dietary specialization. We thus conclude that changes to the neuromuscular control of
46 the neck, not morphological adaptations, are primarily responsible for tripodal locomotion in
47 parrots. We argue that many-to-one mapping of form to function allows parrots with similar neck
48 morphologies to participate in a range of behaviors, and this may be a common feature amongst all
49 birds.

50 **Introduction**

51 The avian forelimb is characterised by its highly specialised anatomy that allows for powered flight.
52 As a consequence of this derived structure and function, it is generally maladapted for many
53 functions outside of this key innovation (1–3). As such a large number of functions that were
54 ancestrally performed by the forelimb are instead shifted to the craniocervical system (i.e., beak,
55 head, and neck) in birds. Thus, the neck of birds functions across a broad range of activities as a
56 ‘surrogate forelimb’ (3–5). Psittaciformes (parrots) exemplify the functional diversity of the avian
57 cervical column as the necks of this group participate in feeding, preening, tool use and most
58 spectacularly, locomotion (6–8). By utilising the neck and head as a third ‘propulsive limb’ parrots
59 are able to ascend vertical and traverse horizontal substrates by co-opting the craniocervical system
60 to function within a cyclical tripodal gait pattern (6,8,9). This adaptation of the craniocervical system
61 to function as a propulsive limb appears to be an evolutionary novelty unique to parrots, and
62 investigating this phenomenon may offer insight into how the head and neck can be exapted to
63 actively participate in locomotion.

64 The use of non-appendicular appendages in locomotion is well-documented across tetrapods. If one
65 of these appendages displays an interaction between the animal’s mass and the substrate then it
66 can be defined as ‘effective limb’ (10). There are numerous examples of portions of the axial column
67 (particularly the tail) acting as an effective limb, however many of these are interacting with the
68 substrate in an incidental manner (e.g. tail dragging (11–13)), or acting as a stabiliser/brace (6).
69 Propulsive limbs (i.e., effective limbs that are used for propulsion (6)) are much rarer in tetrapods
70 and are often limited to the involvement of a tail in powered pentapedal gaits (14,15). Recent work
71 has highlighted the extraordinary ability of Psittaciformes to use the craniocervical system as a
72 propulsive limb, with the beak, neck and hindlimbs generating more relative tangential substrate
73 reaction forces than the forelimbs of humans and primates during vertical climbing (6,8,16). A large
74 proportion of this propulsive force must be driven by the neck as the thoracolumbar spine of birds is
75 adapted for stiffness and stability, not force production (6). This has led to the hypothesis that either
76 the neuronal (6,16) or musculoskeletal system of the psittaciform neck has undergone radical
77 changes to accommodate tripodal locomotion. If the adaptation is neuronal then many-to-one
78 mapping of form to function may be a key component of neck evolution in parrots, allowing novel
79 forms of locomotion to evolve rapidly without the need for large shifts in neck morphology across
80 the entire cervical spine. Parrots may have utilised many-to-one mapping over the course of their

81 evolutionary history to allow them to use their neck in a locomotory capacity without sacrificing the
82 diverse functionality that the 'surrogate forelimb' provides (4). If the adaptation is musculoskeletal,
83 then these changes can be observed by quantifying relationships between vertebral morphology and
84 neck usage in parrots.

85 Many-to-one mapping is a vital concept within evolutionary biology as it can result in a decoupling of
86 functional diversity from morphological diversity within a clade (17,18). This decoupling allows for
87 one morphological trait to accommodate multiple functions, and highlights that the morphological
88 form does not always directly correlate with function (17,19). Many-to-one mapping may be
89 exemplified by the avian neck as it performs a wide range of functions despite a similarity in its
90 overall structure between species, and this is evidenced by recent work which observed that the
91 regional modularity of the avian neck is conserved across many species, only adapting to highly
92 specialised functions such as carnivory (3,20). Here we investigate whether the psittaciform neck
93 breaks this pattern of conservatism in avian neck morphology in order to adapt to function during
94 locomotion, or if many-to-one mapping and changes to neuronal control of parrot neck musculature
95 are responsible for this novel behaviour.

96 Parrots have long been known to engage in climbing behaviour and tripodal locomotion during
97 climbing is thought to be a universal feature of Psittaciformes (21–23). Yet this ubiquity of tripodal
98 locomotion in parrots is anecdotal (21) and the extent of beak-assisted climbing in this clade has
99 never been quantified. By using a framework set out by recent research into avian foot use (24) we
100 can leverage enormous photographic databases of parrots identified to species level in order to
101 quantitatively determine the incidence of beak-assisted climbing across a broad range of extant
102 Psittaciformes. We then use the incidence of climbing data to assess any potential form-function
103 relationships between neck vertebral morphology and beak-assisted climbing. As the psittaciform
104 neck provides much of the propulsive force associated with climbing (6) we hypothesize that a
105 significant portion of vertebral shape variation will be governed by the incidence of beak-assisted
106 climbing. We may further speculate that the selective pressures potentially imposed by beak-
107 assisted climbing upon the neck leads to morphological convergence of the cervical spine in groups
108 that are frequently observed carrying out this behaviour. Prior work can be used as a basis for this
109 hypothesis, and has observed that non-psittaciform birds that share specialised neck kinematics (e.g.
110 carnivorous birds) display similar patterns of gross neck morphology (3). Phenotypic Integration, the
111 co-evolution of anatomical traits, is an important facilitator of morphological diversity and has been
112 found to be an important component of avian skull evolution (25,26). Integration often occurs when
113 multiple anatomical systems function together during a particular behaviour (27–29), and recent
114 data suggests it is a commonplace amongst extant avians (30). As tripodal locomotion involves the
115 neck and hindlimb working in tandem, we also hypothesize that neck-hindlimb integration will
116 significantly influence morphological variation of neck vertebrae across Psittaciformes.

117 Here we use a combination of geometric morphometrics, phylogenetic comparative methods and
118 behaviour quantification to investigate the relationship between neck usage (with a focus on beak-
119 assisted climbing) and neck vertebral morphology across a phylogenetically broad selection of extant
120 parrots. We also assess the relative contributions of other factors that have previously been found to
121 significantly influence the morphological variability of neck vertebral morphology, such as body size,
122 phylogeny, ecology, and morphological integration. Finally, we will use recently established
123 convergence metrics to test for convergence in the vertebral morphology parrots that frequently
124 undertake beak-assisted climbing.

125 **Methods**

126 **Specimen details**

127 We analysed the morphology of the cervical vertebrae, head, forelimb and hindlimb of 48 species of
128 extant parrots (Supplementary Table 1). Neck use behavior was also studied for 44 of 48 of these
129 species. Six of the 48 species were scanned at UCL with a Nikon XT H 225 microCT scanner. Scan data
130 for the remaining 42 species were downloaded from MorphoSource (see Supplementary Table 1 for
131 MorphoSource ID numbers). Dietary and foraging guilds for these species were taken from the
132 AVONET database (31). Phylogenetic trees were acquired from www.birdtree.org and pruned to
133 include only the 48 species included in this study.

134 **Digitisation and 3D geometric morphometrics**

135 Scans for all 48 species were segmented in Amira 3D (version 2021.1, Visualization Science Group,
136 Thermo Fisher Scientific) and the digital models outputted were cleaned and further processed in
137 MeshLab (32). To account for the variation in total cervical vertebral counts between species we
138 analysed 2 homologous vertebrae (the second cervical vertebrae, C2, and the last cervical vertebrae)
139 as well as 3 'functionally homologous' vertebrae (vertebrae at 25%, 50% and 75% along the cervical
140 column) (20,33,34). A vertebral landmark scheme consisting of 22 fixed landmarks (Supplementary
141 Figure 1, Supplementary Table 2) was constructed based on schemes from prior avian vertebral
142 morphometric studies (3,20,35,36). We next calculated head volumes by subjecting digital skull
143 models for each species to an α -shape fitting algorithm that is part of an in-house modified version
144 of the 'alphavol' package for MatLab (3,37). These volumes were then multiplied by the weighted
145 mean densities of soft tissues within the skull (approximated to the density of water, 997 kg/m³).
146 This method may overestimate head mass as it does not model the degree of pneumatic bone and
147 soft tissue within each skull, but such granularity was outside the scope of this study. Head mass was
148 preferred over head shape as head shape often poorly correlates with ecology in birds (25,26,38).
149 We then measured limb element lengths digitally in Geomagic Wrap (Geomagic, United States).
150 Forelimb elements measured include the coracoid, scapula, humerus, radius, ulna and
151 carpometacarpus. Hindlimb elements measured include the femur, tibiotarsus and tarsometatarsus.
152 We size-corrected limb measurements using the following formula: limb element length/body
153 mass^{0.33}. We also size-corrected head mass by calculating the percentage of total body mass. Scaling
154 equations based on the humeral articulation facet of the coracoid were used to estimate body
155 masses (39).

156 **Assessment of neck use behavior**

157 To assess the extent to which the neck was being used by parrots, we devised a scoring system that
158 noted the presence or absence of four neck functions assumed to put relatively high loads on the
159 neck [i.e., beak assisted climbing (6,9,16), forceful flexion and extension (40–42), object carrying)].
160 We used the Macaulay Library (<https://www.macaulaylibrary.org>) to search for images of parrots
161 performing these neck use behaviors following protocols from prior literature (24). Up to 2000
162 images were searched for each of the 48 species in the study (24) (see Supplementary Table 3 for
163 behavior scorings and incidence data). We assessed the relationship between number of photos
164 searched and neck use score for each behavior and found it to be significant for each of the four neck
165 behaviors, as well as for the overall presence or absence of absolute neck use. To accommodate for
166 this we use an incidence of behavior metric that accounts for the number of photos searched.
167 Initially we observed a significant relationship between this incidence metric and the number of
168 photos searched, but after the removal of 4 outliers (species with an unusually high incidence of
169 beak assisted climbing despite < 50 photos searched per species) there was no significant correlation
170 ($p < 0.05$).

171 It should be noted that our method for scoring neck function was a necessity owing to the lack of
172 available quantitative information on neck use in parrots (43). Generally, this approach is
173 synonymous with scan sampling, which provides an unbiased assessment of the activity budget of an
174 animal, but suffers from missing rare or uncommon behaviors (44,45). Indeed, this is confirmed with
175 the relatively low occurrence of neck use observed in parrots in this study (see below). For rare
176 behaviours, focal animal or specific behaviour sampling would be most appropriate (44,45).
177 However, no studies have yet to quantify the positional behaviour of parrots, let alone any non-
178 mammalian species, utilizing such methodology.

179 **Statistical analysis**

180 *Morphological analysis*

181 We first subjected landmark data to Procrustes superimposition. We then performed morphological
182 analyses on a pooled dataset that contained all vertebrae (C2, C25%, C50%, C75% and the last
183 cervical vertebrae) for all species, as well as separate analyses for each vertebral level. This allowed
184 us to study morphological evolution across the entire parrot neck and at the level of individual
185 vertebrae across the cervical spine (20). We calculated multivariate Blomberg's K (K_{mult}) using the
186 function `physig()` within the 'geomorph' R package to estimate the impact of phylogeny on the
187 morphological variation of parrot cervical vertebrae (46). To assess the relationship between
188 vertebral shape variation and ecological parameters, neck use behaviors and body mass we utilized
189 phylogenetic multivariate ANOVAs (pMANOVAs). A reduced dataset was used in the neck use
190 behavior pMANOVAs as we identified some outlier species (see prior methods section, 'Assessment
191 of neck use behavior'). We determined significant differences in morphology between ecological
192 groups using post-hoc pairwise tests with the 'pairwise' function in the 'RRPP' package in R.

193 We identified the degree of head-neck, neck-forelimb and neck-hindlimb integration using a
194 phylogenetic two-block partial least-squares (2BPLS) analysis in the R package 'geomorph' (46). We
195 then used the 'compare.pls' function (as part of the 'geomorph' R package) to search for significant
196 differences in effect sizes across integration tests. Next, we combined all measurements of individual
197 forelimb and hindlimb elements into a single forelimb or hindlimb matrix prior to inclusion in any
198 2BPLS analyses. Following this, we carried out pMANOVAs and 2BPLS tests for a pooled vertebral
199 dataset and for each individual vertebral level. In order to assess differences in morphological shape
200 change across the entire neck we applied Phenotypic Trajectory Analysis (PTA) (47). PTA plots a
201 trajectory through shape space for a particular group (in this case for a particular dietary or foraging
202 category) by connecting the mean shape of a particular vertebrae in a sequential chain from C2 to
203 the last cervical vertebrae. This allows for the statistical assessment of differences between certain
204 groups in the pattern of sequential vertebral shape change across the entire neck.

205 We produced phylomorphospace plots of PC1 and PC2 for each individual cervical vertebrae to
206 visualize differences in morphospace occupation between ecological groups and between disparate
207 incidences of neck use behavior values. We focused on exploring these axes because for each
208 vertebra, the subsequent PC axes each explained < 30% of the overall variation in each ordination.
209 We used these phylomorphospace plots to inform our hypotheses for morphological convergence
210 analyses. These visualizations allowed us to identify focal taxa that share the same ecology or neck
211 use traits and also occupied a distinct area of morphospace and were thus candidates for convergent
212 evolution. We then tested for morphological convergence using the Ct1-Ct4 metrics using the
213 'calcConvCt' and 'calcSigCt' functions in the R package 'convevol' (48,49).

214 *Behavior analysis*

215 Following the protocol of previous work (24) we first tested for any correlation between the number
216 of photos studied versus the overall occurrence of neck use behavior with a PGLS using the 'glsl'
217 function of the R package 'nlme'. The absolute occurrence of neck use displayed a significant
218 correlation with the number of media analysed, and as such we accounted for the number of media
219 by using an incidence of neck use metric. We used Phylogenetic ANOVAs to assess potential
220 correlations between the incidence of neck use behaviors and ecological categories, body mass and
221 head mass. We visualized the distribution of the incidence of neck use behavior across our sample by
222 mapping this trait onto a phylogenetic tree using the 'contMap' function in 'phytools' (50).

223

224 **Results**

225 **Morphological variation of parrot neck vertebrae**

226 Three out of five of the studied cervical vertebrae occupy distinct areas of morphospace when all
227 vertebrae are projected onto the same morphospace, with only C50% and C75% displaying any level
228 of overlap (Supplementary Figure 4). Principal component (PC) 1 accounts for 38.15% of the
229 morphological variation and higher PC1 scores are associated with a lengthening of the centrum and
230 vertebral arch, a decrease in size of the neural spine, a widening of the neural canal and vertebral
231 arch, and an increase in length of the costal processes (Supplementary Figure 4). PC2 accounts for
232 27.63% of the morphological variation, with higher PC2 scores corresponding to a decrease in
233 centrum and vertebral arch length, an increase in neural spine height, a narrower neural canal, more
234 robust prezygapophyses and transverse processes, a widening of pre- and post-articular facets and an
235 increase in the size of the ventral spine (Supplementary Figure 4).

236 We then ordinated morphological variation for each vertebrae individually, revealing two distinct
237 patterns for either proximal or distal vertebrae. Proximal vertebrae (C50%, C75% and the last cervical
238 vertebrae) tended to display elongated and deeper centrums along the main axis of variation (PC1),
239 whilst centrum length shortened across PC1 for more distal vertebrae (C2 and C25%). PC1
240 corresponds to between 21.4% (C25%) and 43.78% (C75%) of the vertebral morphological variation,
241 and PC2 corresponds to between 11.27% (C2) and 16.28% (C50%) of vertebral morphological
242 variation (Figure 1). Increases to values of PC1 of C2 vertebrae correspond to a shortening of the
243 centrum and vertebral arch, an increase in height and width of the neural spine, more robust
244 zygapophyses and a reduction in size of both articular facets (Figure 1). An increase in PC2 scores of
245 C2 vertebrae is associated with a shortening and narrowing of both the centrum and vertebral arch
246 alongside an increase in neural spine height (Figure 1). Increases to PC1 scores of C25% vertebrae
247 correspond to a widening and shortening of the centrum and vertebral arch, a small increase in
248 height of both the neural and ventral spines, and a reduction in the height of the postarticular facet
249 (Figure 1). Increases to PC2 values correspond to subtle changes in C25% morphology such as a less
250 posteriorly pronounced ventral lip of the postarticular facet and a slight reduction in costal process
251 length (Figure 1). For middle (C50%) vertebrae, increases in PC1 scores are associated with a slight
252 increase in the length and depth of the centrum, a posterior shift in the position of the neural spine,
253 a narrowing of the transverse processes, shorter postzygapophyses and elongated costal processes
254 (Figure 1). Increases to PC2 scores in middle vertebrae are associated with an increased neural spine
255 height and enlarged transverse processes (Figure 1). Changes in vertebral shape across PC1 in C75%
256 vertebrae correspond to an increased centrum depth, a slight increase in neural spine height, a
257 minor elongation of the costal processes, and a more concave postarticular surface (Figure 1).
258 Increases in PC2 scores in C75% vertebrae are associated with increases to the width of both the
259 transverse processes and the postzygapophyses (Figure 1). For the last cervical vertebrae changes

260 associated with increased PC1 scores correspond to an increase in centrum length and depth,
261 increases to neural and ventral spine height, narrower transverse processes, more dorsally
262 positioned prezygapophyses and narrower postzygapophyses (Figure 1). Shape changes associated
263 with an increase in PC2 scores of the last cervical vertebrae correspond to a more anteriorly
264 positioned postzygapophysis and an enlarged postarticular facet (Figure 1).

265 **Allometric and phylogenetic signal in parrot neck morphology**

266 There is a significant relationship between body mass and vertebral shape in the pooled dataset ($p =$
267 0.004) as well as in C2 ($p = 0.001$), C25% ($p = 0.002$) and the last cervical vertebrae ($p = 0.035$)
268 (Supplementary Table 4). However, the proportion of morphological variation that can be explained
269 by body mass alone is small and varies between 0.044 (last cervical vertebrae) and 0.075 (C2)
270 (Supplementary Table 4). We calculated K_{mult} to determine the strength and significance of the
271 phylogenetic signal on the morphological variation of parrot cervical vertebrae. A significant ($P <$
272 0.05) and weak-to-moderate (lowest K_{mult} C2 = 0.496, highest K_{mult} last = 0.672) phylogenetic signal
273 can be observed in the morphological variation of the pooled vertebral dataset, as well as for all but
274 one (C75%, $p = 0.111$, $K_{mult} = 0.479$) of the individual cervical regions.

275 **Ecological signal in parrot neck morphology**

276 Results from the pMANOVAs suggest significant differences exist in morphology between dietary
277 groups within the pooled dataset ($p = 0.004$), as well as within C2 ($p = 0.004$), C25% ($p = 0.014$) and
278 C75% ($p = 0.014$) vertebrae (Supplementary Table 4). Diet displayed a weak correlation with vertebral
279 shape across all vertebrae studied (R^2 between 0.121 in C25% and 0.151 in C75%), yet displayed a
280 comparatively higher coefficient of correlation than body mass (R^2 0.045 – 0.075) (Supplementary
281 Table 4). Foraging guild displayed no significant correlation ($P > 0.05$) with vertebral morphology
282 across any of the vertebral regions studied (Supplementary Table 4). This weak ecological and
283 phylogenetic signal in parrot cervical morphology is reflected in the lack of distinction between
284 ecological and family-level groups in morphospace across all vertebral regions studied.

285 A post-hoc pairwise test revealed that between dietary groups, terrestrial herbivores and granivores
286 often displayed significantly different vertebral morphologies compared to most other dietary groups
287 (Supplementary Table 5). Terrestrial herbivores often displayed significant differences in vertebral
288 morphology compared to other dietary groups (8 comparisons across C2, C25% and C75%)
289 (Supplementary Table 5). Vertebral morphology was significantly different between herbivores and
290 frugivores in C2 ($p = 0.043$) and C25% ($p = 0.049$), between herbivores and generalists in C2 ($p =$
291 0.04), C25% ($p = 0.04$) and C75% ($p = 0.017$) and between herbivores and nectarivores in C2 ($p =$
292 0.012), C25% ($p = 0.015$) and C75% ($p = 0.02$) (Supplementary Table 5). Multiple dietary groups also
293 displayed significant differences in vertebral morphology when compared to granivores, including
294 nectarivores (C2 $p = 0.026$ and C25% $p = 0.044$) and generalists (C75%, $p = 0.032$) (Supplementary
295 Table 5). Terrestrial herbivores had predominantly taller neural spines than other dietary groups
296 across C2, C25% and C75%, a shortened centrum in C25% and a deeper centrum in C75%. Granivores
297 also display a taller neural spine across C2, C25% and C75%, as well as comparatively deeper centra
298 in C2 and C75%.

299 PTA detected that across all dietary, foraging and neck-use groupings, patterns of whole-neck
300 morphological variation were only significantly different between a select few dietary groups
301 (Supplementary Table 6). We tested for pairwise differences between dietary, foraging and
302 phylogenetic groupings separately and found only 4 dietary pairwise comparisons to be significant
303 (Supplementary Table 6, Supplementary Figure 4). Trajectory shape was significantly different

304 between terrestrial herbivores and generalists ($p = 0.02$), as well as between terrestrial herbivores
305 and granivores ($p = 0.035$) (Supplementary Table 6). The magnitude of differences between
306 trajectories was significant between generalists and frugivores ($p = 0.035$), as well as between
307 generalists and granivores ($p = 0.005$) (Supplementary Table 6).

308 **The influence of neck use on parrot neck morphology**

309 Our survey of neck use across 44 species of parrots (excluding outliers, see Methods) revealed that
310 across 40,893 images studied, the incidence of absolute neck use was 0.638%. Across each individual
311 neck use behavior, average incidence varied between 0.450% for beak-assisted climbing and 0.032%
312 for object carrying (Supplementary Table 3). Numerous species (out of 48 total) were never observed
313 performing each behavior and this value ranged between 13 and 14 in absolute incidence of neck
314 use and beak assisted climbing and 40 in forceful extension (Supplementary Table 3). Before
315 evaluating the relationship between the incidence of neck use behaviors and cervical morphology,
316 we assessed the relationship between behavior, body mass, head mass and ecology (diet and
317 foraging guild). Across all behaviors only the overall incidence of absolute neck use was significantly
318 correlated with body mass ($p < 0.001$) and head mass ($p = 0.002$), beak assisted climbing was also
319 significantly correlated with head mass only ($p = 0.016$) (Supplementary Table 7).

320 We investigated potential correlations between the incidence of each neck use behavior and cervical
321 vertebral morphology for the pooled dataset as well as for each individual cervical region.
322 Consequently, we found a significant, weak correlation between the incidence of total neck use and
323 the morphology of C2 vertebrae ($p = 0.034$, $R^2 = 0.042$), as well as similarly weak correlation between
324 incidence of beak assisted climbing and C2 vertebral morphology ($p = 0.043$, $R^2 = 0.039$)
325 (Supplementary Table 7). Species that have a high incidence of beak assisted climbing rarely occupy
326 distinct areas of morphospace (except for C2), and often coincide with species with minimal or no
327 occurrences of beak assisted climbing (Figure 2, Supplementary Figure 4). These high incidence
328 climbers also do not occupy similar areas of morphospace, often appearing far apart from each other
329 in all studied morphospaces (Figure 2, Supplementary Figure 4). Convergence tests revealed that
330 species with a high incidence of beak assisted climbing and total neck use were not convergent ($P >>$
331 0.05). We then visually identified smaller subsets (or pairs) of species with high incidence of neck use
332 behaviors or the same dietary guild that occupied similar areas of phylomorphospace and repeated
333 the convergence tests. None of these further convergence tests were significant ($P >> 0.05$).

334

335 **The effects of integration on parrot cervical morphology**

336 Parrots display significant integration across all of three of the studied regimes ($P < 0.05$ for head-
337 neck, neck-forelimb and neck-hindlimb integration, Supplementary Table 8). R PLS values were
338 generally high and ranged from 0.847 for head-neck integration across all vertebrae to 0.522 for
339 neck-forelimb integration in the last cervical vertebrae (Supplementary Table 8). Whereas R PLS
340 values and Z scores seem to decrease towards the proximal end of the cervical column, there are no
341 significant differences between Z scores for integration tests for different vertebrae. Many integrative
342 relationships are not significant when head, forelimb or hindlimb measures are adjusted for body
343 mass (Supplementary Table 8). Only the last cervical vertebrae retains a significant pattern of neck-
344 forelimb integration when adjusted for body mass (Supplementary Table 8). Significance is retained
345 in the pooled dataset, C50% and the last cervical vertebrae for head-neck integration, and no
346 vertebral region retains significance after adjusting hindlimb measurements for body mass
347 (Supplementary Table 8). Across all integration regimes studied, a gradient of body mass can be

348 observed whereby parrots with high body masses displayed extreme values of PLS1 and PLS2 and
349 parrots with low body mass clustered together at the other extreme of PLS1 and PLS2 (Figure 3).

350

351 **Discussion**

352 Here we present the results of the first study to investigate factors that have influenced the
353 morphological variation of psittaciform cervical vertebrae, as well as results from the first study to
354 quantify neck use across Psittaciformes. We find that variation in the morphology of parrot neck
355 vertebrae is governed by a variety of factors including phylogeny, allometry, ecology and integration
356 with both the head and forelimb. Contrary to prior anecdotal evidence, we find that beak-assisted
357 climbing is not a ubiquitous behavior across Psittaciformes and was not observed in 14 of the 48
358 species studied. Furthermore, we find that a weak but significant relationship exists between the
359 incidence of beak-assisted climbing and the morphological variability of psittaciform C2 vertebrae
360 (Figure 2, Supplementary Table 7). We were also able to qualitatively and quantitatively demonstrate
361 that beak-assisted climbing is not responsible for any convergence in the morphology of cervical
362 vertebrae amongst parrots with similar incidences of this behavior (Figure 2, Supplementary Figure
363 4). The neck of parrots also displays significant integration with the head, forelimb and hindlimb
364 however these integrative relationships often disappear when body mass is accounted for
365 (Supplementary Table 8).

366 Evolution of morphological form is often multifactorial in nature due to the interplay of phylogenetic
367 constraints, allometry, ecology and integration with other anatomical components (26–28,51).
368 Indeed, both evolutionary allometry (phylogeny and body size) and phenotypic integration have
369 previously been shown to be some of the factors that influence skull shape variation in parrots (26).
370 The factors that influence morphological variation are therefore broadly similar across the head and
371 neck of Psittaciformes as phylogeny, body mass, and integration all significantly influence the shape
372 variation of the psittaciform neck. A key difference between the skull and neck of parrots is that
373 dietary preference accounts for more morphological variation in the neck of parrots (up to 15% vs
374 2.4%, Supplementary Table 4). We had expected to observe the opposite pattern as the skull directly
375 manipulates and processes food, not the neck (7,26,52,53). Diet is still a minor (~15%) component of
376 neck morphological variation however, and the differences observed here may be due to
377 discrepancies in dietary classification schemes between the two studies (26). Allometry accounted
378 for a smaller proportion of cervical shape variation than diet (between 4.4% and 7.5%), however it
379 evidently plays an important role in the integrative relationships between the neck, head and
380 appendicular skeleton as the significance of head-neck, neck-forelimb and neck-hindlimb integration
381 often disappears when body mass is taken into account (Supplementary Table 8). Across many of
382 these integrative relationships we observed that larger parrots clustered together with extreme PLS1
383 and PLS2 scores (Figure 3) and this clustering may indicate that body mass may be a controlling
384 factor in psittaciform neck integration. Since beak-assisted climbing requires the cooperation of the
385 psittaciform craniocervical and hindlimb skeleton, a coordinated morphological response may be
386 required in order for this multi-body system behavior to occur in larger parrots (16,51,54–56).

387

388 Across multiple morphological scales we observe that parrots with different diets and neck use
389 behaviors often have similar neck morphologies (Figures 1 & 2, Supplementary Tables 4–7) and we
390 infer this is a feature of many-to-one mapping (18,19). Although we do observe a significant
391 relationship between diet, neck use and vertebral morphology, we find that these relationships are

392 weak (Supplementary Table 4) and that dietary and neck use groups often heavily overlap in
393 morphospace (Figures 1 & 2). We also find very few significant differences between the pattern of
394 morphological variation across the entire neck among dietary and behavioral groups (Supplementary
395 Table 6). The neck of parrots provides much of the propulsion during beak-assisted climbing. Indeed,
396 kinematic data suggests it is capable of producing relatively greater contractile forces than the
397 human neck (6,57). It has also been anecdotally reported that all parrots engage in this behavior
398 (21). In response to this we hypothesized that beak-assisted climbing would be a highly influential
399 factor in the morphological variance of the cervical column across Psittaciformes, and that this
400 behavior was leading to morphological convergence of cervical vertebrae. In light of the present
401 results, we reject this hypothesis and suggest that form and function are somewhat decoupled in the
402 psittaciform cervical column. Instead of a tight relationship between form and function, we suggest
403 that many-to-one mapping of form to function is allowing parrots to occupy a diverse range of
404 dietary niches and to utilize a wide array of neck use behaviors (18,19), including tripodal locomotion
405 (6,16) and 'beakiation' (9). By displaying neither significant morphological convergence or clear
406 morphological adaptations to dietary ecology or neck use we hypothesize that changes to muscle
407 activation patterns and neuromuscular innovation may be responsible for tripodal locomotion and
408 array of neck use behaviors in Psittaciformes, as has previously been suggested (6,16). The
409 neuromuscular pathways associated with neck use behaviors such as beak-assisted climbing must
410 allow for movements of the craniocervical system to be incorporated into the locomotor cycle (6).
411 This may not require a radical neuromuscular innovation as this pathway already exists to
412 accommodate avian head-bobbing (58), and may have been modified by parrots to allow for tripodal
413 locomotion (6,16). Since the neuromuscular pathways associated with the parrot neck are already
414 optimized for a wide variety of behaviors, these pathways may display plasticity in their ability to
415 adapt to novel functions such as beak-assisted climbing (6,16) and 'beakiation' (9).

416 The findings presented here for parrots may have implications for the mechanisms behind broader
417 avian neck evolution, as the ecological signal in cervical morphological variation is similarly low
418 across Aves (3,20,30). The similarly weak influence of ecology on neck morphology across all birds
419 suggests that many-to-one mapping may be present across Aves. This extrapolation could explain
420 why there is an apparent disconnect between avian cervical form and function: the overall
421 morphological construction of the avian neck is highly conserved and only adapts to behaviors that
422 require specialized kinematic forces, yet the neck still participates in a disparate array of behaviors
423 (3,4). Although further work is required to formally test the presence of many-to-one mapping in the
424 parrot and avian cervical column, it has been shown to be a common feature of organismal design
425 (18,19) that weakens the effect of convergent evolution (59).

426 Conclusions

427 This work represents the first quantification of the presence of tripodal locomotion across parrots
428 and finds that beak-assisted climbing is not a ubiquitous feature of Psittaciformes. We also find that
429 tripodal locomotion, alongside a multitude of other factors, governs a small portion of morphological
430 variability of the parrot neck. Parrots with similar cervical morphologies appear to be able to use
431 their necks to access a wide variety of food types and to both participate and not participate in beak-
432 assisted climbing. This suggests that many-to-one mapping of cervical form to function is a feature of
433 the neck of Psittaciformes, and potentially a feature of neck construction across extant Aves. Without
434 the presence of clear vertebral adaptations to beak-assisted climbing we suggest changes to the
435 neuromuscular control of the cervical column have underpinned the evolution of tripodal
436 locomotion in parrots and this may be a modification of existing neural pathways associated with
437 avian head-bobbing.

438 Figures & tables

439 Figure 1: Morphospaces for each of the psittaciform cervical regions studied, grouped by dietary
440 preference. A) C2 cervical vertebrae, B) C25% cervical vertebrae, C) C50% vertebrae, D) C75%
441 vertebrae, E) Last cervical vertebrae. Warped meshes of cervical vertebrae display changes across
442 PC1 and PC2 in anterior (left along PC1, bottom along PC2) view and left lateral (right along PC1, top
443 along PC2) view.

444 Figure 2: Phylomorphospace of PC1 and PC2 for the C2 vertebrae of parrots. Points are coloured by
445 incidence of beak-assisted climbing. Next to the 4 species of parrot that experience the highest
446 incidence of BAC are photographs of that species as well as the mesh of that species' C2 vertebrae.
447 Bottom photo: *Lathamus discolor* (photo credit David Irving, Macaulay Library ID ML613044549).
448 Bottom-left photo: *Psittacus erithacus* (photo credit Manuel-Fernandez-Bermejo, Macaulay Library
449 ID ML613685886). Top photo: *Rhynchositta pachyrhyncha* (photo credit Ken Chamberlain, Macaulay
450 Library ID ML608581146). Right photo: *Oreopsittacus arfaki* (photo credit Robert Tizard, Macaulay
451 Library ID ML613799167).

452 Figure 3: 2BPLS plots of vertebral shape versus forelimb proportion (Ai-Av), vertebral shape versus
453 head mass (Bi-Bv) and vertebral shape versus hindlimb proportion (Ci-Cv). Arrows beside the Y-axes
454 indicate what portion of the limb is increasing as PLS2 scores increase: purple denote the proximal
455 portion is lengthening and yellow indicates the distal portion is lengthening. Points within each
456 2BPLS plot are coloured by body mass. Warped meshes of cervical vertebrae for each plot display
457 shape changes across PLS1. The forelimb is represented by *Ara ararauna* in A, the skull morphology
458 displayed in B is that of *Micropsitta finschii*, the hindlimb is represented by *Chalcopsitta atra* in C.

459 Supplementary Figure 1: Visual representation of the landmark scheme used throughout this study.
460 Mesh is the C25% vertebrae of *Pionites melanocephalus*.

461 Supplementary Figure 2: Morphospace of vertebral shape across the neck of all parrots studied.
462 Colours denote vertebral region. Warped meshes of cervical vertebrae display shape change across
463 PC1 and PC2 in anterior (left along PC1, bottom along PC2) view and left lateral (right along PC1, top
464 along PC2).

465 Supplementary Figure 3: Phenotypic trajectory plot depicting patterns of shape change across the
466 neck of parrots with different dietary niches. Point and line colours denote dietary preference and
467 point shape denotes vertebral region.

468 Supplementary Figure 4: Phylomorphospace plots for the C25% (A), C50% (B), C75% (C) and last
469 cervical vertebrae (D) of 44 species of parrots. Points are coloured by incidence of beak-assisted
470 climbing.

471 Supplementary Table 1: Specimen information and metadata for all studied species. Asterisks
472 indicate outlier taxa that were removed from the neck use incidence analysis.

473 Supplementary Table 2: Landmark scheme used as part of the geometric morphometric component
474 of this analysis.

475 Supplementary Table 3: Neck-use behaviour data for all species. Asterisks indicate outlier taxa that
476 were removed from the neck use incidence analysis.

477 Supplementary Table 4: Results from the pMANOVA (phylogenetic multivariate ANOVA) analyses.

478 Supplementary Table 5: Results summary of post-hoc tests performed after pMANOVA.

479 Supplementary Table 6: Results summary of the phenotypic trajectory analysis (PTA). MD =
480 magnitude of differences between trajectories, TC = trajectory correlations, SD = trajectory shape
481 differences.

482 Supplementary Table 7: Behavioural MANOVA results table

483 Supplementary Table 8: 2BPLS results table

484

485 **References**

- 486 1. Heers AM, Dial KP. From extant to extinct: locomotor ontogeny and the evolution of avian flight.
487 Trends in Ecology & Evolution. 2012 May 1;27(5):296–305.
- 488 2. Marek RD. The Surrogate Arm: Functional Morphology of the Avian Cervical Column [Internet]
489 [Ph.D.]. [England]: The University of Liverpool (United Kingdom); 2020 [cited 2023 Aug 31].
490 Available from:
491 <https://www.proquest.com/docview/2451874026/abstract/9CB75106C01A45B2PQ/1>
- 492 3. Marek RD, Falkingham PL, Benson RBJ, Gardiner JD, Maddox TW, Bates KT. Evolutionary
493 versatility of the avian neck. Proceedings of the Royal Society B: Biological Sciences. 2021 Mar
494 3;288(1946):20203150.
- 495 4. Marek RD. A surrogate forelimb: Evolution, function and development of the avian cervical
496 spine. Journal of Morphology. 2023;284(10):e21638.
- 497 5. Bhullar BAS, Hanson M, Fabbri M, Pritchard A, Bever GS, Hoffman E. How to Make a Bird Skull:
498 Major Transitions in the Evolution of the Avian Cranium, Paedomorphosis, and the Beak as a
499 Surrogate Hand. Integrative and Comparative Biology. 2016 Sep 1;56(3):389–403.
- 500 6. Young MW, Dickinson E, Flaim ND, Granatosky MC. Overcoming a ‘forbidden phenotype’: the
501 parrot’s head supports, propels and powers tripodal locomotion. Proceedings of the Royal
502 Society B: Biological Sciences. 2022 May 18;289(1975):20220245.
- 503 7. Young MW, Wilken AT, Manafzadeh AR, Schurr AF, Bastian A, Dickinson E, et al. The dual function
504 of prokinesis in the feeding and locomotor systems of parrots. Journal of Experimental Biology.
505 2023 Dec 8;226(24):jeb246659.
- 506 8. Reader LL, Carrier DR, Goller F, Isaacs MR, Moore Crisp A, Barnes CJ, et al. Climbing parrots
507 achieve pitch stability using forces and free moments produced by axial–appendicular couples.
508 Journal of Experimental Biology. 2022 Jan 7;225(1):jeb242305.
- 509 9. Dickinson E, Young MW, Granatosky MC. Beakiation: how a novel parrot gait expands the
510 locomotor repertoire of living birds. Royal Society Open Science. 2024 Jan 31;11(1):231397.
- 511 10. Bertram JE. Concepts in locomotion: levers, struts, pendula and springs. Understanding
512 mammalian locomotion: concepts and applications. 2016;79–109.
- 513 11. Willey JS, Biknevicius AR, Reilly SM, Earls KD. The tale of the tail: limb function and locomotor
514 mechanics in *Alligator mississippiensis*. Journal of Experimental Biology. 2004 Jan 22;207(3):553–
515 63.

516 12. Pridmore P. Submerged walking in the epaulette shark *Hemiscyllium ocellatum* (Hemiscyllidae)
517 and its implications for locomotion in rhipidistian fishes and early tetrapods. *Zoology*.
518 1994;98:278–97.

519 13. Zinner D, Fickenscher G, Roos C, Mittermeier R, Rylands A, Wilson D. *Handbook of the mammals*
520 of the world. Primates. 2013;

521 14. O'Connor SM, Dawson TJ, Kram R, Donelan JM. The kangaroo's tail propels and powers
522 pentapedal locomotion. *Biology letters*. 2014;10(7):20140381.

523 15. Schmitt D, Rose MD, Turnquist JE, Lemelin P. Role of the prehensile tail during ateline
524 locomotion: experimental and osteological evidence. *American Journal of Physical Anthropology*:
525 The Official Publication of the American Association of Physical Anthropologists.
526 2005;126(4):435–46.

527 16. Young MW, Webster C, Tanis D, Schurr AF, Hanna CS, Lynch SK, et al. What does climbing mean
528 exactly? Assessing spatiotemporal gait characteristics of inclined locomotion in parrots. *J Comp*
529 *Physiol A* [Internet]. 2023 May 4 [cited 2023 Oct 24]; Available from:
530 <https://doi.org/10.1007/s00359-023-01630-0>

531 17. Alfaro ME, Bolnick DI, Wainwright PC. Evolutionary Consequences of Many-to-One Mapping of
532 Jaw Morphology to Mechanics in Labrid Fishes. *The American Naturalist*. 2005 Jun;165(6):E140–
533 54.

534 18. Wainwright PC, Alfaro ME, Bolnick DI, Hulsey CD. Many-to-One Mapping of Form to Function: A
535 General Principle in Organismal Design?1. *Integrative and Comparative Biology*. 2005 Apr
536 1;45(2):256–62.

537 19. Wainwright PC. Functional Versus Morphological Diversity in Macroevolution. *Annual Review of*
538 *Ecology, Evolution, and Systematics*. 2007;38(1):381–401.

539 20. Marek RD, Felice RN. The neck as a keystone structure in avian macroevolution and mosaicism.
540 *BMC Biology*. 2023 Oct 13;21(1):216.

541 21. Dilger WC. The comparative ethology of the African parrot genus *Agapornis*. *Zeitschrift für*
542 *Tierpsychologie*. 1960;

543 22. Brockway BF. Ethological studies of the budgerigar (*Melopsittacus undulatus*): Non-reproductive
544 behavior. *Behaviour*. 1964;22(3–4):193–222.

545 23. Webster C, Jusufi A, Liu D. A comparative survey of climbing robots and arboreal animals in
546 scaling complex environments. In Springer; 2019. p. 31–45.

547 24. Gutiérrez-Ibáñez C, Amaral-Peçanha C, Iwaniuk AN, Wylie DR, Baron J. Online repositories of
548 photographs and videos provide insights into the evolution of skilled hindlimb movements in
549 birds. *Commun Biol*. 2023 Aug 15;6(1):1–11.

550 25. Bright JA, Marugán-Lobón J, Cobb SN, Rayfield EJ. The shapes of bird beaks are highly controlled
551 by nondietary factors. *Proceedings of the National Academy of Sciences*. 2016 May
552 10;113(19):5352–7.

553 26. Bright JA, Marugán-Lobón J, Rayfield EJ, Cobb SN. The multifactorial nature of beak and skull
554 shape evolution in parrots and cockatoos (Psittaciformes). *BMC Evolutionary Biology*. 2019 May
555 17;19(1):104.

556 27. Goswami A, Smaers JB, Soligo C, Polly PD. The macroevolutionary consequences of phenotypic
557 integration: from development to deep time. *Philos Trans R Soc Lond B Biol Sci*. 2014 Aug
558 19;369(1649):20130254.

559 28. Felice RN, Randau M, Goswami A. A fly in a tube: Macroevolutionary expectations for integrated
560 phenotypes. *Evolution*. 2018 Dec 1;72(12):2580–94.

561 29. Evans KM, Larouche O, Watson SJ, Farina S, Habegger ML, Friedman M. Integration drives rapid
562 phenotypic evolution in flatfishes. *Proceedings of the National Academy of Sciences*. 2021 May
563 4;118(18):e2101330118.

564 30. Böhmer C, Plateau O, Cornette R, Abourachid A. Correlated evolution of neck length and leg
565 length in birds. *Royal Society Open Science*. 2019 May 8;6(5):181588.

566 31. Tobias JA, Pigot AL. Integrating behaviour and ecology into global biodiversity conservation
567 strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2019 Jul
568 29;374(1781):20190012.

569 32. Cignoni P, Callieri M, Corsini M, Dellepiane M, Ganovelli F, Ranzuglia G. Meshlab: an open-source
570 mesh processing tool. In Salerno, Italy; 2008. p. 129–36.

571 33. Jones KE, Benítez L, Angielczyk KD, Pierce SE. Adaptation and constraint in the evolution of the
572 mammalian backbone *O6 Biological Sciences*. *BMC Evolutionary Biology*. 2018;18(1).

573 34. Jones KE, Dickson BV, Angielczyk KD, Pierce SE. Adaptive landscapes challenge the “lateral-to-
574 sagittal” paradigm for mammalian vertebral evolution. *Current Biology*. 2021 May 10;31(9):1883-
575 1892.e7.

576 35. Böhmer C, Rauhut OWM, Wörheide G. Correlation between Hox code and vertebral morphology
577 in archosaurs. *Proceedings of the Royal Society B: Biological Sciences*. 2015 Jul
578 7;282(1810):20150077.

579 36. Terray L, Plateau O, Abourachid A, Böhmer C, Delapré A, de la Bernardie X, et al. Modularity of
580 the Neck in Birds (Aves). *Evol Biol*. 2020 Jun 1;47(2):97–110.

581 37. Brassey CA, Gardiner JD. An advanced shape-fitting algorithm applied to quadrupedal mammals:
582 improving volumetric mass estimates. *Royal Society Open Science*. 2015 Aug;2(8):150302.

583 38. Navalón G, Bright JA, Marugán-Lobón J, Rayfield EJ. The evolutionary relationship among beak
584 shape, mechanical advantage, and feeding ecology in modern birds*. *Evolution*. 2019 Mar
585 1;73(3):422–35.

586 39. Field DJ, Lynner C, Brown C, Darroch SAF. Skeletal Correlates for Body Mass Estimation in
587 Modern and Fossil Flying Birds. *PLOS ONE*. 2013 Nov 29;8(11):e82000.

588 40. Ramírez-Herranz M, Sayol F, Ríos RS, Antonelli A, Squeo FA. The origin of excavator nesting
589 behavior and its impact on the evolution of Neotropical parrots. *Oikos*. 2024;n/a(n/a):e10155.

590 41. Romero-Vidal P, Blanco G, Hiraldo F, Díaz-Luque JA, Luna Á, Lera D, et al. Nesting innovations in
591 neotropical parrots associated to anthropogenic environmental changes. *Ecology and Evolution*.
592 2023;13(9):e10462.

593 42. Brightsmith DJ. Competition, predation and nest niche shifts among tropical cavity nesters:
594 phylogeny and natural history evolution of parrots (Psittaciformes) and trogons (Trogoniformes).
595 *Journal of Avian Biology*. 2005;36(1):64–73.

596 43. Granatosky MC, Young MW, Herr V, Chai C, Raidah A, Kairo JN, et al. Positional Behavior of
597 Introduced Monk Parakeets (*Myiopsitta monachus*) in an Urban Landscape. *Animals*. 2022
598 Jan;12(18):2372.

599 44. Lehner PN. Design and Execution of Animal Behavior Research: An Overview. *Journal of Animal
600 Science*. 1987 Nov 1;65(5):1213–9.

601 45. Altmann J. Observational Study of Behavior: Sampling Methods. *Behaviour*. 1974 Jan 1;49(3–
602 4):227–66.

603 46. Adams DC, Otárola-Castillo E. geomorph: an R package for the collection and analysis of
604 geometric morphometric shape data. *Methods in ecology and evolution*. 2013;4(4):393–9.

605 47. Collyer M, Adams D. Phenotypic trajectory analysis: comparison of shape change patterns in
606 evolution and ecology. 2013;

607 48. Stayton CT, Stayton MCT. Package ‘convevol.’ 2015;

608 49. Grossnickle DM, Brightly WH, Weaver LN, Stanchak KE, Roston RA, Pevsner SK, et al. Challenges
609 and advances in methods for measuring phenotypic convergence [Internet]. bioRxiv; 2023 [cited
610 2023 Oct 2]. p. 2022.10.18.512739. Available from:
611 <https://www.biorxiv.org/content/10.1101/2022.10.18.512739v3>

612 50. Revell LJ. phytools: an R package for phylogenetic comparative biology (and other things).
613 *Methods in Ecology and Evolution*. 2012;3(2):217–23.

614 51. Marroig G, Shirai LT, Porto A, de Oliveira FB, De Conto V. The Evolution of Modularity in the
615 Mammalian Skull II: Evolutionary Consequences. *Evol Biol*. 2009 Mar 1;36(1):136–48.

616 52. Snively E, Russell AP, Powell GL, Theodor JM, Ryan MJ. The role of the neck in the feeding
617 behaviour of the Tyrannosauridae: inference based on kinematics and muscle function of extant
618 avians. *Journal of Zoology*. 2014;292(4):290–303.

619 53. van der Leeuw AHJ, Bout RG, Zweers GA. Control of the Cranio-Cervical System During Feeding in
620 Birds1. *American Zoologist*. 2001 Dec 1;41(6):1352–63.

621 54. Hildebrand M, Bramble DM, Liem KF, Wake DB. *Functional vertebrate morphology*. Harvard
622 University Press; 1985.

623 55. Cant JG. Positional behavior and body size of arboreal primates: a theoretical framework for field
624 studies and an illustration of its application. *American journal of physical anthropology*.
625 1992;88(3):273–83.

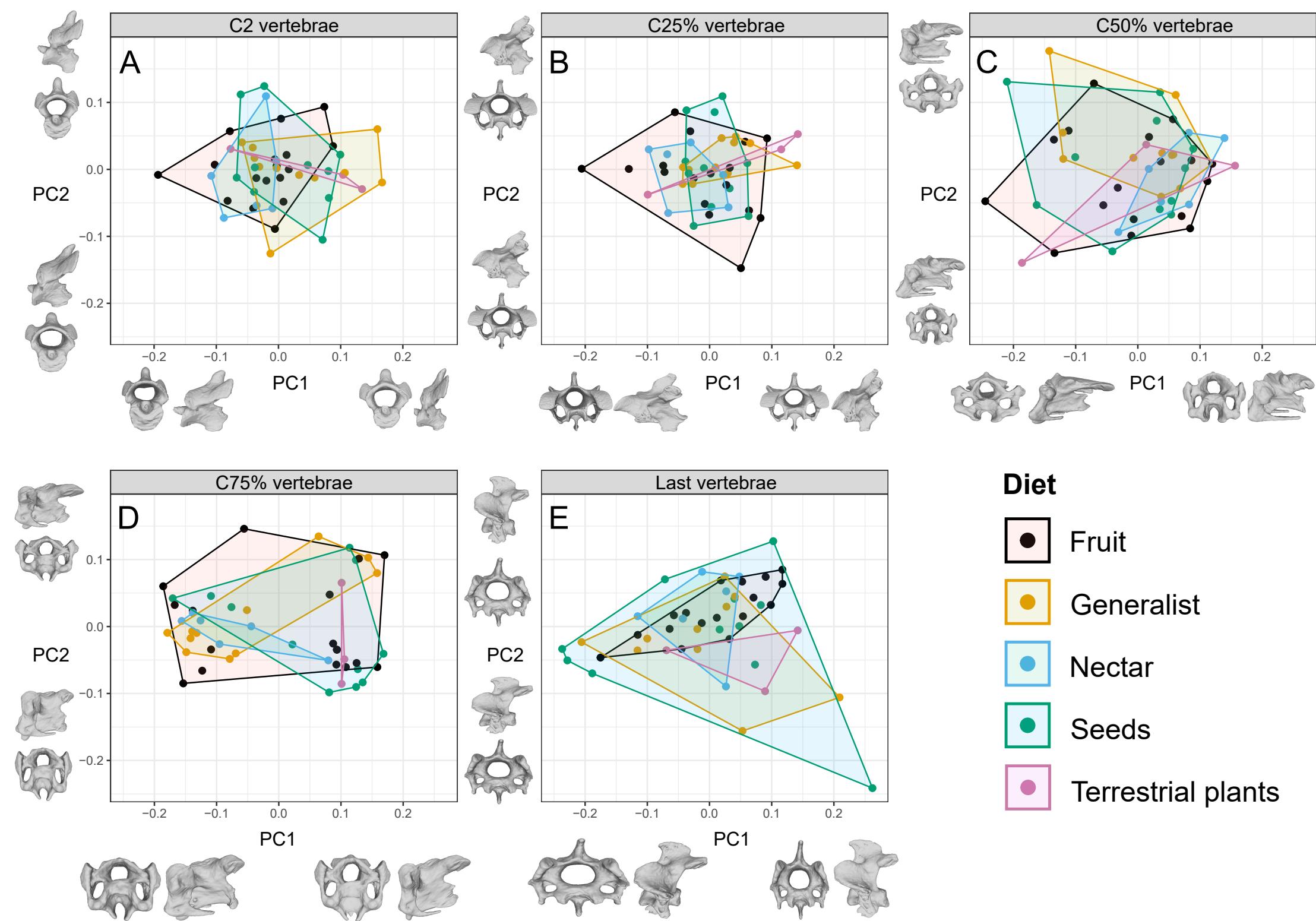
626 56. Granatosky MC. A review of locomotor diversity in mammals with analyses exploring the
627 influence of substrate use, body mass and intermembral index in primates. *Journal of Zoology*.
628 2018;306(4):207–16.

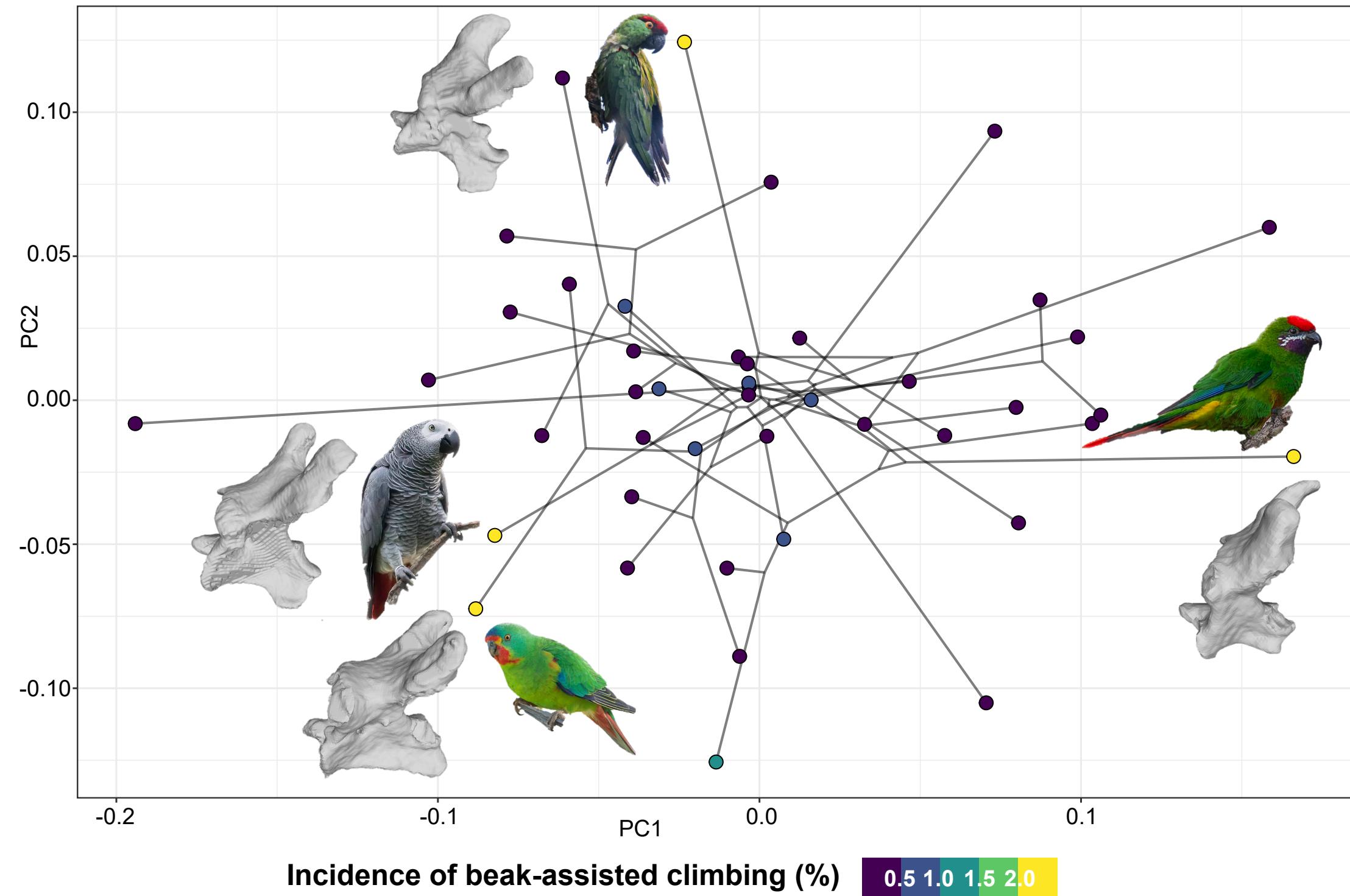
629 57. Valkeinen H, Ylinen J, Mälkiä E, Alen M, Häkkinen K. Maximal force, force/time and
630 activation/coactivation characteristics of the neck muscles in extension and flexion in healthy
631 men and women at different ages. *European journal of applied physiology*. 2002;88:247–54.

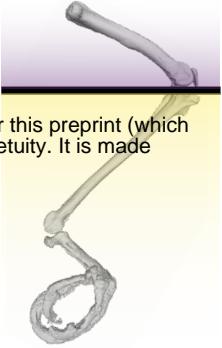
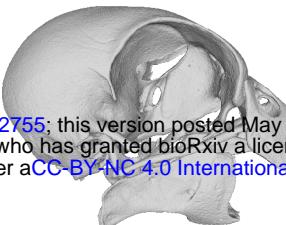
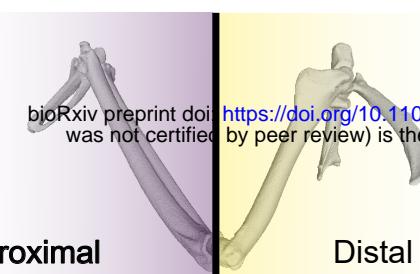
632 58. Nyakatura JA, Andrada E. On vision in birds: coordination of head-bobbing and gait stabilises
633 vertical head position in quail. *Frontiers in zoology*. 2014;11:1–10.

634 59. Thompson CJ, Ahmed NI, Veen T, Peichel CL, Hendry AP, Bolnick DI, et al. Many-to-one form-to-
635 function mapping weakens parallel morphological evolution. *Evolution*. 2017 Nov
636 1;71(11):2738–49.

637







A diagram of a long bone, likely a humerus, oriented vertically. The proximal end is on the left, and the distal end is on the right. The shaft of the bone is shaded in purple, while the epiphyses (proximal and distal ends) are shaded in yellow. The word "Proximal" is written in black text to the left of the proximal end, and "Distal" is written in black text to the right of the distal end.

