1   **The Use of Biogeographical Patterns to Assess Key Adaptations in Two Families of Birds**

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Abstract

28   Adaptations can be thought of as evolutionary technologies that allow organisms to

29   exploit their environment. Like human technologies, adaptations can be 'progressive', increasing

30   in their ability to accomplish a task. Progressive adaptations which also fundamentally alter the

31   rules of trade-offs are known as key adaptations. Key adaptations allow a taxon to expand its

32   niche space thereby radiating to larger species numbers and spread beyond its original range. If

33   so, then of two otherwise ecologically equivalent taxa, the one with the greater geographical

34   range may have a key adaptation. We tested this hypothesis by comparing the global

35   biogeographic patterns of hummingbirds (Trochilidae) and sunbirds (Nectariniidae), ecologically

36   equivalent families with distinct evolutionary technologies. Though many species of both

37   families feed on nectar, hummingbirds also possess adaptations permitting hovering flight. We

38   analyzed each family's species diversity with latitude and elevation, charting how they decline

39   with movement towards poles and peaks. Hummingbirds persist into higher elevation and more

40   extreme latitudes than sunbirds, reaching their 50% species richness value at 22.14° and 2087 m

41   versus 18.92° and 2533 m for sunbirds. Looking at morphology, the evolution of hovering is

42   likely the constraint breaking adaptation that allowed hummingbirds to radiate into more species

43   and inhabit more extreme climes than sunbirds. Comparing the biogeography of ecologically-

44   equivalent taxa has the potential to reveal insights into the species adaptations and niche

45   expansion.

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Introduction

The traits possessed by a species govern the types of environments it can exploit – its fundamental niche. Evolution by natural selection shapes the traits of species to optimize fitness by tailoring an organism's morphology, physiology, and behavior to their environments (Darwin, 1859). Such traits – or adaptations – can be thought of as "evolutionary technologies" that allow an organism to operate within an environment. An organism's adaptations add up to a suite of technologies that allows it to persist in its fundamental niche. As many habitats across the world display remarkable similarity in environmental condition, species within these similar habitats have evolved similar adaptations, a process known as convergent evolution (Mooney and Dunn, 1970). If the full suite of evolutionary technologies of multiple different species are similar enough to each other and the species exist within similar niches, the species are deemed to be ecological equivalents, species that occupy a similar fundamental niche space and fulfill similar functional roles (Biggins et al., 2011). Examples are found within taxa as diverse as weasels (Biggins et al., 2011), desert snakes, rodents (Montgomery, 1989; Mares, 1975), and epiphytes (Bennet, 1986).

Like human technologies, evolutionary technologies are not perfect in their ability to accomplish a task, these imperfections relaying costs to the organism. The costs may be concrete – such as the energy and material needed to maintain the adaptation – or abstract – such as the lack of information that comes from a less than perfect adaptation (Kotler and Mitchell, 1995). The costs derived from evolutionary technologies lead to trade-offs that a species must negotiate if it is to optimize its fitness. Yet like human technologies, evolutionary technologies can be progressive, increasing their ability to accomplish a specific task (Dawkins, 1997). If an adaptation is not only progressive but also fundamentally changes the rules of the trade-offs, it is

70   known as a key adaptation (Rosenzweig and McCord, 1991; Galis, 2001). An example of a key

71   adaptation would be the evolution of wood. To grow taller, plants must accumulate tissue to

72   support the extra weight. Wood, a non-living tissue, allows plants to grow taller without the need

73   maintain the tissue. Trade-offs are not eliminated – it takes much longer to create wood

74   compared to living tissue – but instead altered such that woody plants are favored in

75   environments with infrequent disturbance.

76   Looking across evolutionary history, the evolution of a key adaptation often leads to the

77   radiation of a new, more speciose clade – now defined by its synapomorphy – often replacing the

78   older, ecologically-equivalent clade from which it came. This replacement process – known as

79   incumbent replacement – has been seen in turtles (Rosenzweig and McCord, 1991), native and

80   introduced marsh snails (Berman and Carlton, 1991), spiriferacean brachiopods (McGhee, Jr.,

81   1981) and more. More importantly, the evolution of adaptations which reduce the cost of trade-

82   offs allow the clade to expand niche space and corresponding biogeographical range (Holt et al.,

83   1997). This effect can be seen with the *Peromyscus* and *Apodemus* genera of mice. *Peromysucus*

84   has a better and more widely used torpor state which allows species within the genera to inhabit

85   colder, more arid, and elevationally higher habitats compared to the ecologically equivalent

86   genus *Apodemus* (Morhardt, 1970; Walton and Andrews, 1981; Motngomery, 1989). With this

87   relationship of key adaptations leading to more speciose clades with a larger geographical extent,

88   it may imply the reverse: among ecologically equivalent clades, the one with the greatest species

89   richness and biogeographical range should possess superior evolutionary technologies.

90   One test of the presence of key adaptations within a clade has been to compare the

91   species richness between taxa (Galis, 2001). However, of the two properties of species richness

92   and biogeographical extent that define a clade, biogeographical extent is theoretically more

93   useful when comparing strength of evolutionary technologies: the larger the biogeographical

94   extent, the greater the range of environmental and ecological variables with which a clade has to

95   deal in most cases. Therefore, any comparison between taxa based upon biogeographical extent

96   more explicitly compares the strength of the evolutionary technology within the clades and the

97   possibility of key adaptations versus simple species richness alone. Comparing biogeography

98   should work best when comparing extant, non-sympatric, ecologically equivalent taxa due to an

99   incomplete fossil record and the possibility of competition otherwise.

100   While there is extreme variation in many biogeographic patterns, latitudinal and

101   elevational gradients in species richness are robust geographic patterns found among nearly all

102   taxa (Terborgh, 1977; Graham, 1983; Rosenzweig, 1995; Kaufman, 1995; Sánchez-Cordero,

103   2001; Sanders, 2002; Hillebrand, 2004). Generally, as one moves from low latitudes or

104   elevations towards the poles and higher elevations respectively, the species richness of a taxon

105   declines. Numerous properties change along the two gradients. Both gradients show declines in

106   productivity and temperature averages and increases in seasonal temperature variation. Only

107   species with superior evolutionary technologies are able to mitigate the costs of colder

108   temperatures and reduction of exploitable resources (Buckley et al., 2012). Elevational gradients

109   also include the properties of declining atmospheric pressure, an especially critical resource for

110   metazoans, and increasing daily temperature variation. These additional factors mean that taxa

111   should show a clearer response to elevation dependent upon their evolutionary technologies.

112   To this end, we analyzed at the latitudinal and elevational distribution of two convergent

113   families of nectarivorous birds, hummingbirds (Trochilidae) and sunbirds (Nectariniidae), to see

114   if and what their biogeography can tell us about the strength of their adaptations. Both families

115   show adaptations to a nectarivorous environment, namely elongated bills and tongues with

116   lamellae-like structures, with the hummingbirds displaying a stronger mutualistic co-adaptation

117   with flowers compared to sunbirds, suggesting the presence of a key adaptation within the taxon

118   (Johnsgard, 1997, Cheke and Mann, 2001). These features, combined with the hemispheric

119   separation and differences in species richness, indicate that hummingbirds and sunbirds are well-

120   suited for biogeographic comparisons to determine key adaptation strength. In this study, we

121   seek to ask several questions. Do hummingbirds extend farther latitudinally and elevationally

122   than sunbirds? What does the shape of their distribution tell us about their interactions with the

123   environment? And more generally, will a difference in biogeography and species richness

124   between ecologically equivalent taxa indicate the presence of a key adaptation in one of the taxa?

125   **Materials and Methods**

126   Study Families

127   Hummingbirds (order Apodiformes, family Trochilidae) and sunbirds (order

128   Passeriformes, family Nectariniidae) are two families of nectarivorous birds. There are

129   approximately 365 hummingbird species all located in the New World (BirdLife International,

130   2015) with a latitudinal extent from Alaska to Argentina. Hummingbirds are the most specialized

131   of all the nectar feeding birds, all feeding almost exclusively on nectar and only supplementing

132   protein intake by eating small insects (Yanega and Rubega, 2004). Due to this tight co-

133   adaptations between food and forager, hummingbirds have evolved distinct anatomical and

134   morphological features suited to nectar foraging. Such features include elongated bills and

135   extensile, bifurcated, tubular tongues that acts as micro-pumps for reaching and gathering nectar,

136   large breast muscles (30% of body weight) and specialized wings giving them the ability to

137   hover and fly backwards, and a dense erythrocyte count delivering a steady supply of oxygen to

138   feed extremely active muscles (Johnsgard, 1997; Rico-Guevera and Rubega, 2011; Rico-Guevera

139   et al., 2014).

140   One-hundred-twenty-four sunbird species (family Nectariniidae) exist worldwide

141   (BirdLife International, 2015). All of them occur in the Old World, specifically Africa, mainland

142   Asia, the Indonesian Archipelago, and much of Australasia. Their latitudinal range stretches from

143   the southern tip of Australia to as far north as Lebanon and the Himalayas. Though the family of

144   sunbirds contain a large number of nectar feeders, the co-adaptation between food and forager is

145   not as tight as hummingbirds. Many species will supplement their diet with insects, seeds, fruit,

146   and flower heads. As expected, there is large variation in morphology based on each species'

147   relationship with nectar. Sugarbirds and most true sunbirds have long bills with some adapted

148   specific flower species and long, tubular, bifurcated tongues with serrated edges similar to

149   hummingbirds. Flowerpeckers and the *Hedydipna* and *Hypogramma* sunbirds have broad, flat

150   tongues as they are less specialized to nectar feeding. Though some species can hover in front of

151   flowers when feeding, sunbirds generally lack the breast muscle architecture found in

152   hummingbirds with most perching to feed; those less specialized to nectar feeding will typically

153   nectar-rob, entering the flower through the side rather than the front (Cheke and Mann, 2001).

154   Methods

155   To determine the presence of key adaptations within the family of hummingbirds, we

156   assessed the latitudinal and elevational gradients of both families. Besides the expected

157   relationship with the strength of adaptations, latitudinal and elevational gradients have many

158   features that make particularly useful for this analysis. Firstly, the commonality of latitudinal and

159   elevational gradients of species richness brings a robustness and consistency to the analysis by

160   standardizing the comparison. Secondly, spatial comparisons over a wide geographic range are

161   better able to indicate the presence of key adaptations as they cover many environmental

162   variables – reducing the chance of a false negative – but are not inherently correlated to the

163   adaptation in question – preventing false positives. (Admittedly, spatial analysis does not tell us

164   what the key adaptation is or what it is adapted towards, something which looking at a suite of

165   environmental variables would indicate). Additionally, elevational comparisons offer a stronger

166   comparison between families. This is because a purely random process of range size and position

167   determination within a bounded geographical space of a group of species will generate a hump-

168   shaped gradient resembling, but not similar to, latitudinal gradients (Willig and Lyons, 1998).

169   Elevational gradients occur in bounded geographical space but present a skewed distribution

170   indicating the lack of random processes. Therefore, any difference between the families is almost

171   definitely an effect of their natural histories.

172   To create latitudinal and elevational gradients with which compare the two families, we

173   used the latitudinal and elevational range of each species. Elevational ranges were taken from a

174   database on the ecology and biogeography maintained by Çağan H. Şekercioğlu and used as is.

175   Two different latitudinal gradients were analyzed: latitude as is and "polewardness," a measure

176   of distance from the equator. Latitudinal ranges of the families were taken from shapefiles

177   downloaded from BirdLife International (2015) – data extracted using R – and used for the first

178   measure as is except for converting southern latitudes to negative values. To create the second

179   measure of polewardness, the maximal and minimal latitudinal range of each species was

180   extracted and rounded up and down respectively to the nearest integer. For example, the

181   hummingbird species *Amazilia amabilis* which ranges from 14.17N to 3.98S would have its

182   range modified to 15N and 4S. If the range then crossed the equator, then the range was taken to

183   be from 0 to the maximum distance from the equator, effectively 'folding' the range at the

184   equator.. In the previous example, this would mean the poleward range would be 0 to 15 degrees.

185   A species which exists only in the Northern or Southern hemisphere would simply have its

186   poleward range as the absolute value of its latitudinal range.

187   With the latitudinal, poleward, and elevational ranges, we analyzed the families in two

188   ways. First, we compared several empirical cumulative distribution functions (ECDFs) based

189   upon the three geographical properties (elevation, latitude, and polewardness) for each family. To

190   create the ECDFs, we assumed a species to be present depending upon three different points in

191   the range: the minimum, maximum, and central points. Central points were usually determined

192   by taking the midpoint of each range which assumes a symmetrical abundance distribution. Since

193   polewardness had the folding property, we created an extra measure of centrality, expected

194   polewardness. For species whose ranges crossed the equator, we assumed that abundance was

195   stacked creating a new distribution (abundance was assumed to be uniform for easier

196   calculation). We then calculated the expected value of this stacked uniform distribution seen in

197   eq. (1) where min and max stand for the absolute value of minimum and maximum latitude

198   respectively.

199
$$\frac{1}{2} * \frac{min^2 + max^2}{(min + max)} \qquad \text{(Equation 1)}$$

200   This lead to ten different ECDFs for each family: minimum elevation, maximum

201   elevation, midpoint elevation, minimum latitude, maximum latitude, midpoint latitude, minimum

202   polewardness, maximum polewardness, midpoint polewardness, and expected polewardness.

203   Each type of ECDF was then compared between families using two different minimum

204   difference estimation (MDE) tests, the Kolmogorov-Smirnov and Anderson-Darling tests, with

205   the assumption that of hummingbird ECDF is less than the sunbird ECDF (one-tailed tests). We

206   feel that the ECDFs based upon central points were most accurate as they were neither under nor

207   over conservative. This method of analysis tells us with statistical certainty whether the

208   distributions differ, though not necessarily how they differ.

209   Second, to characterize each family's distribution, we intervals of 5 degrees for

210   polewardness and half kilometers for elevation and counted the number of species for each

211   family in each interval. If a species' range was the cutoff point of the interval, it would be

212   considered as present in the lower interval but not in the upper interval due to previous rounding.

213   In the example with *A. amabilis*, this would mean that the species would exist in the 10 to 15

214   degree interval but not the 15 to 20 degree interval. With the data on the two families' species

215   richness vs the two ranges, the data were then normalized such that the interval with the highest

216   number of species became 1 to remove the effect of species richness. This gave us four sets of

217   data based on a 2x2 factorial: sunbird and hummingbird vs. latitude and elevation. A logistic

218   function (eq. 2) was then fitted onto each of the four sets of data – the proportional species

219   richness, S_p, per interval vs. the midpoint of each interval – with variables a and b determining

220   position and steepness respectively.

221     $$S_P = \frac{1}{1 + a e^{bx}}$$ (Equation 2)

222   With each function characterized, we then found the specific inflection points (eq. 3),

223   which corresponded to the point at which species richness was half of maximum species

224   richness, and the roots of the third derivative (jerk points) (eq. 4) and points of maximum

225   magnitude of curvature (MMC points), both of which corresponded to the start and end of the

226   decline of species richness. Since MMC points have no explicit solution, we instead estimated

227   them by searching over the positive number line with R. Using these points, we characterized

228   how species richness declines in each family with elevation and polewardness.

229 $$x = \frac{1}{b} \log \left(\frac{1}{a} \right)$$ (Equation 3)

230 $$x = \frac{1}{b} \log \left(\frac{2 \pm \sqrt{3}}{a} \right)$$ (Equation 4)

231   This second method of analysis with functions and points now characterize the shape of

232 each family's gradient.

Results

234   Broadly, our results show that hummingbirds extend further poleward and higher in

235 elevation than sunbirds. Hummingbirds extend from as far north as 62 degrees to as far south as

236 56 degrees and up to 5000m in elevation. Sunbirds, on the other hand, extend only from 36

237 degrees north to 40 degrees south and up to 4880m in elevation (Table 1). Both families show the

238 same general pattern of initial increase in species richness from the equator and sea-level, both

239 reaching their maximum in the 5-10 degree and 500-1000m intervals, before declining (Fig. 2).

240 Inspecting the figures, we can see that hummingbirds are able to maintain proportional species

241 richness at higher levels than sunbirds but in different ways with regards to elevation and

242 latitude.

ECDF Results

244   The ECDF results broadly show that hummingbird and sunbird distributions differed

245 across all measures (Table 2). The only measures that returned values of non-significance were

246 the measures based upon the maximum latitude of each species' range. The centrality based

247 ECDFs all returned significant values. Elevational ECDFs gave the greatest degree of difference

248 and the smallest p-values, followed by poleward ECDFs, then simple latitude ECDFs. With the

249 confirmation of difference in elevational and latitudinal distributions between hummingbirds and

250 sunbirds, we turn to characterizing the differences.

251 <u>Elevation</u>

252   Both hummingbirds and sunbirds reach approximately the same maximum elevation,

253 around 5000m (Table 1a, Fig. 2a). With our fitted functions, we see that even though both

254 hummingbirds and sunbirds extend to roughly the same elevation, hummingbirds are able to

255 maintain higher proportional species richness at higher elevations compared to sunbirds. For

256 sunbirds, the relationship with elevation is $S_P = {}^1\!/_{1\,+\,0.006546e^{2.409634*\mathrm{ELEV}}}$; for

257 hummingbirds, $S_P = {}^1\!/_{1\,+\,0.02024e^{1.53943*\mathrm{ELEV}}}$ (Table 3). Looking at the inflection points, we

258 see that sunbirds reach 50% of maximum species richness at 2087m in elevation with

259 hummingbirds reaching theirs at 2533m. Sunbirds and hummingbirds both start their decline

260 around the same elevation – 1540m and 1678m respectively using the jerk, 1764 and 1898m

261 using MMCs – but sunbirds end their decline at a lower elevation compared to hummingbirds –

262 2634m vs. 3385m respectively according to the jerk, 2410m vs. 3458m according to the MMCs –

263 indicating a more gradual decline in proportional species richness for hummingbirds (Table 4,

264 Fig 2b.).

265 <u>Latitude</u>

266   Unlike the case of elevation, hummingbirds reach further from the equator than sunbirds,

267 60-65 degrees vs. 35-40 degrees respectively (Table 1b, Fig. 2b). Also unlike elevation,

268 hummingbird proportional species richness is at its greatest divergence from sunbird

269 proportional species richness at mid-latitudinal ranges. For hummingbirds, the relationship

270 equation is $S_P = {}^1\!/_{1\,+\,0.019757e^{0.177253*\mathrm{ELEV}}}$ and for sunbirds,

271    $S_P = {}^1\!/_{1\,+\,0.077829e^{0.134976*\mathrm{ELEV}}}$ (Table 3). Hummingbirds reach 50% S_p at 22.14 degrees

272 latitude, later than the 18.92 degrees of sunbirds. Hummingbirds also begin their declines later

273 than sunbirds – 14.71 and 9.16 degrees respectively using the jerk, 14.99 and 9.44 degrees using

274   MMC. Both stop the decline around the same latitude – 29.57 vs. 28.67 degrees according to the

275   jerk, 29.29 vs. 28.39 degrees according to the MMC – confirming the steeper but later decline of

276   hummingbirds (Table 4, Figure 2d).

277   **Discussion**

278   Sunbirds and hummingbirds are two convergent nectarivorous families of birds with

279   various evolutionary technologies for their feeding operations. While hummingbirds are

280   extremely specialized to their nectar feeding diet, sunbirds vary in specialization ranging from

281   the hummingbird-like sugarbirds to the passerine-like flowerpeckers (Johnsgard, 1997; Cheke

282   and Mann, 2001). These differences in evolutionary technologies should reflect differences in the

283   respective families' distribution and biogeography. Species richness of hummingbirds show

284   greater resilience compared to sunbirds as one moves higher in elevation and away from the

285   equator. With regards to elevation, hummingbirds and sunbirds extend to the same elevational

286   height, approximately 5000m, but proportional hummingbird species richness holds up much

287   better at higher elevations when compared with sunbirds, declining at a slower rate until they

288   reach the same species richness at 5000m. With regards to latitude, though not as striking a

289   difference, hummingbirds do show greater robustness compared to hummingbirds, especially

290   noting that hummingbirds extend further north and south than sunbirds. Our results give

291   additional evidence to the correlation between a taxa's species richness and geographic range.

292   One potential hypothesis for the differences in biogeography between hummingbirds is

293   dispersal limitation. In the Old World, many of the mountain ranges run along the east-west axis

294   while New World mountains run in a north-south manner. The Old World mountains may form

295   barriers which prevent sunbirds from extending as far north as hummingbirds; certainly, lack of

296   land prevents sunbirds from extending as far south. We, though, reject the dispersal limitation

297   argument on two key grounds. Firstly, hummingbirds are still more speciose than sunbirds. Of

298   the 365 species, only 15 hummingbirds are found in the latitudinal range where sunbirds are not.

299   Even if we assume that expansion into the northern latitudes led to the creation of all 15 species,

300   it still only accounts for approximately 4% of hummingbird species. Clearly the differences in

301   species richness of the families are not due to range expansion. This implies that greater

302   geographic range followed greater speciosity and not vice-versa if dispersal limitation were a

303   factor. Secondly, hummingbirds are able to deal well with mountains. Not only do hummingbirds

304   maintain species richness at higher elevations as our study showed, they have higher species

305   richness in the mountains of western North and South America compared to the flat-lying eastern

306   regions and frequently migrate along these routes. Instead, we feel that the evidence is highly

307   suggestive of one or more key adaptations in hummingbirds.

308   There are many similarities between hummingbirds and highly specialized sunbirds,

309   making them ecological equivalents, but they do differ in specific areas. It is within these

310   differences where hummingbirds' key adaptation should lie. Likely, the key adaptation deals with

311   the manner of foraging, specifically feeding and flight. With regard to feeding, one possibility for

312   hummingbirds' key adaptation may be their unique tongues. The tongues of hummingbirds have

313   recently been shown to act as micropumps, a way of quickly and efficiently gathering nectar

314   from flowers versus the previous assumption of capillary action (Rico-Guevera and Rubega,

315   2011; Rico-Guevera et al., 2014). This unusual method of nectar-gathering may allow

316   hummingbirds to more efficiently gather nectar compared to sunbirds. Not enough is known

317   about sunbird tongues though to see how the two taxa compare in nectar gathering abilities.

318   Studies indicate that hummingbirds and sunbirds gather nectar at seemingly comparable rate

319   suggesting that the amount gathered is not the key difference (Hainsworth, 1973; Schlamowitz et

320   al., 1976; Paton and Collins, 1989; Rico-Guevera et al., 2014 [pers. calc.]). If the tongue is the

321   key adaptation, then it will be for the fact that micropumping requires no energy expenditure on

322   the part of hummingbirds – removing a cost – while sunbirds apparently intake nectar through

323   suction – a potentially energetically expensive system (Liversidge, 1967; Downs, 2004). Much

324   more research needs to be done on the tongues of sunbirds to see how they compare with the

325   tongues of hummingbirds.

326   Another possibility of the key adaptation that separates hummingbirds and sunbirds is

327   hummingbird's ability to hover and fly in all directions more efficiently (Johnsgard, 1997).

328   Adaptations for a hovering lifestyle include shortened arm bones (humerus, ulna, and radius) and

329   longer hand bones, a relatively fixed V-shaped arm position, a shallow ball-and-cup joint

330   between the coracoid and sternum, a large sternum with a deep keel onto which large breast

331   muscles – pectoralis and supracoracoideus – attach, and red-blood cells and hemoglobin adapted

332   for higher-oxygen affinity and carrying capability (Schuchmann, 1999; Chantler, 1999; Warrick

333   et al., 2012; Zusi, 2013). All these anatomical features are adaptations to stiff-winged flight and

334   seen to a lesser extreme within other bird families of the order Apodiformes (Schuchmann, 1999;

335   Chantler, 1999; Zusi, 2013). What truly differentiates the flight of hummingbirds is the axial

336   rotation of the humerus and wrist bones during flight (Zusi, 2013). Hummingbirds are able to

337   create lift on the upstroke – in addition to the downstroke seen in all birds – due to wing

338   inversion caused by axial rotation of the wrist (Warrick et al., 2012). Wrist flexibility comes from

339   changes in carpal structure and deletion of key ligaments and is seen in birds outside of

340   Apodiformes (Ros et al., 2011; Zusi, 2013; Parslew, 2015). In addition, additional power to each

341   downstroke and upstroke comes from axial rotation of humerus, driven by the pectoralis,

342   supracoracoideus, and other muscles (Hedrick et al., 2012; Warrick et al., 2012; Zusi, 2013). The

343   humerus is able to rotate up to 180º due to a unique humeroscapular joint (Ingram, 1978;

344   Schuchmann, 1999). The key adaptation of this joint is the placement of the humeral head along

345   the axis of the shaft instead of the terminal position, a feature only seen in hummingbirds (Karhu,

346   1999; Videler, 2006). Together, this suite of adaptations allows hummingbirds to hover

347   effectively when foraging.

348   It is currently unknown what the benefits to hovering may be. We speculate three possible

349   reasons. Firstly, hummingbirds may be able to exploit the nectar of plants without perches,

350   potentially opening up a new resource for them. As most nectarivorous birds need to perch while

351   feeding, flowers without perches may represent a relatively abundant and constant resource

352   without competition from other similar species. Evolution of hovering in this scenario may be a

353   virtuous cycle as other hovering becomes more efficient at high nectar volumes which occur in

354   the absence of competition (Dreisig, 1997). Secondly, hummingbirds may be able to escape

355   predation due to their unique flying abilities. With the ability to fly in all directions,

356   hummingbirds may be easily avoid predators, a useful ability especially when feeding at a flower

357   with blocked sightlines (Lima, 1993). Finally, while hovering is energetically costly, it is also

358   time efficient (Hainsworth, 1986). Hovering birds spend less time gathering resources at flowers

359   than birds which rely on perches. This means that hovering becomes more energetically efficient

360   compared to perching when birds feed within clustered flower patches (Pyke, 1981; Wolf and

361   Hainsworth, 1983). The suite of evolutionary technologies may also benefit hummingbirds in

362   secondary ways. For example, hummingbirds are able to sustain flight more efficiently at higher

363   altitudes, likely due to their denser erythrocyte count, expanding their fundamental niche to

364   higher elevations (Berger, 1974). What is clear though is that a hummmingbird's adaptations for

365   hovering – in particular, the movement of the humeral head from a terminal to axial position –

366   fundamentally changes the rules of their nectarivory; they exist as a new type of bauplan while

367   sunbirds are still effectively a fancy passerine (Rosenzweig and McCord, 1991; Vincent and

368   Brown, 2005). Coupling the fact that almost no hummingbird species is not a highly specialized

369   nectarivore while many sunbirds range in their specialization with species richness and

370   biogeographic data suggest hummingbirds have incumbently replaced their ancestral-type that

371   was less specialized to nectar feeding.

372   There could be many reasons why hummingbirds developed their key adaptation.

373   Hummingbirds underwent an expansive radiation during the uplift of the Andes beginning

374   around 10mya (McGuire et al., 2014). Living in such harsh conditions could have necessitated

375   the evolution of a more efficient foraging system. As mentioned earlier, greater oxygen capacity

376   is beneficial to both hovering and living in low oxygen conditions. There is also the possibility

377   that the rise of the Andes freed up niche space that would have otherwise been taken up by a

378   competing family like hawkmoths (Sphingidae), a sort of ecological and evolutionary constraint

379   (Halloway et al., 201X). Furthermore, sunbirds may face their own internal constraints, genetic

380   or otherwise, preventing them from evolving a key adaptation (Arnold, 1992). Whatever the case

381   may be, the evolution of this adaptation allowed hummingbirds to more efficiently take

382   advantage of a resource and expand their species number and geographical range.

383   By comparing the biogeography of two convergent families of organisms, we can gain

384   insight into the difference in evolutionary technologies between them. A taxon with higher

385   species richness and a larger geographical range than its equivalent sister taxa is likely to have a

386   key adaptation that allows it to achieve such species numbers and range extent. One possible

387   example could be the American and European earthworms. European earthworms, having been

388   introduced to North America, have colonized parts of North America that are farther north than

389   their American counterparts (Frelich et al., 2006). Both earthworms are ecological equivalents

390   and have convergent features to fill the role of soil turners. This greater range could potentially

391   mean that the European earthworms have some superior evolutionary technology that allows

392   them to expand their range farther north than the native North American species.

393   Great insights into the nature of adaptations of ecologically equivalent taxa may be

394   deduced from comparison of their geographic ranges. Our study provides a proof-of-concept for

395   this hypothesis.

References

396 Arnold, S.J. 1992. Constraints on phenotypic evolution. The American Naturalist **140**:S85-S107

398 Bennet, B.C. 1986. Patchiness, diversity, and abundance relationships in vascular epiphytes.

399   Selbyana **9**:70-75

400 Berger, M. 1974. Energiewechsel von Kolibris beim Schwirrflug unter Hoehenbedingungen.

401   Journal fuer Ornithologie 115:273-288

402 Berman, J. and J.T. Carlton. 1991. Marine invasion processes: interactions between native and

403   introduced marsh snails. Journal of Experimental Marine Biology and Ecology **150**:267-

404   281

405 Biggins, D.E., L.R. Hanebury, B.J. Miller, and R.A. Powell. 2011. Black-footed ferrets and

406   Siberian polecats as ecological equivalents and ecological surrogates. Journal of

407   Mammalogy **92**:710-720

408 BirdLife International and NatureServe (2015) Bird species distribution maps of the world.

409   BirdLife International, Cambridge, UK and NatureServe, Arlington, USA.

410 Buckley, L., A.H. Hurlbert, and W. Jetz. 2012. Broad-scale ecological implications of ectothermy

411   and endothermy in changing environments. Global Ecology and Biogeography **21:**873-

412   885

413 Chantler, P. 1999. Family Apodidae (Swifts). Pages 388-417 *in* J. del Hoyo, A. Elliot, and J.

414   Sargatal, editors. Handbook of the Birds of the World, Vol.5. Lynx Edicions, Barcelona,

415   Spain.

416 Cheke, R.A. and C.F. Mann. 2001. Sunbirds: A Guide to the Flowerpeckers, Spiderhunters and

417   Sugarbirds of the World. Christopher Helm, London, United Kingdom.

418   Darwin, C. 1859. The origin of species by means of natural selection: or, the preservation of

419   favoured races in the struggle for life. John Murray, London

420   Dawkins, R. 1997. Human chauvinism. Evolution **15**:1015-1020

421   Dreisig, H. 1997. Why do some nectar foragers perch and others hover while probing flowers?

422   Evolutionary Ecology **11**:543-555

423   Frelich, L.E., C.M. Hale, S. Scheu, A.R. Holdsworth, L. Heneghan, P.J. Bolden, and P.B. Reich.

424   2006. Earthworm invasion into previously earthworm-free temperate and boreal forests.

425   Biological Invasions **9**:1235-1245

426   Galis, F. 2001. Key innovations and radiations. Pages 581-605 *in* G.P. Wagner. The character

427   concept in evolutionary biology. Academic Press, San Diego, California, USA

428   Graham, G.L. 1983. Changes in bat species diversity along an elevational gradient up the

429   Peruvian Andes. Journal of Mammalogy **64**:559-571

430   Hainsworth, F.R. 1973. On the tongue of a hummingbird: its role in the rate and energetics of

431   feeding. Comparative Biochemistry and Physiology **46A**:65-78

432   Hainsworth, F.R. 1986. Why hummingbirds hover: a commentary. The Auk **103**:832-833

433   Halloway, A.H., J.S. Brown, and C.J. Whelan. 201X. The hummingbird and the hawkmoth:

434   species diversity, competition, and niche partitioning across the United States.

435   Manuscript

436   Hedrick, T.L., B.W. Toblaske, I.G. Ros, D.R. Warrick, and A.A. Biewener. 2012. Morphological

437   and kinematic basis of the hummingbird flight stroke: scaling of flight muscle

438   transmission ratio. Proceedings of the Royal Society B **279**:1986-1992

439   Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. The American

440   Naturalist **163**:192-211

441   Holt, R.D., J.H. Lawton, K.J. Gaston, and T.M. Blackburn. 1997. On the relationship between

442   range size and local abundance: back to basics. Oikos **78**:183-190

443   Ingram, K. 1978. Hummingbirds and miscellaneous orders (Apodiformes, Caprimulgiformes,

444   Coliiformes, Trogoniformes, Musophagiformes, and Cuculiformes). Pages 335-346 *in*

445   Fowler, M.E., editor. Zoo and Wild Animal Medicine. W.B. Saunder Company,

446   Philadelphia, Pennsylvania, USA

447   Johnsgard, P.A. 1997. The Hummingbirds of North America. Smithsonian Institution Press,

448   Washington, D.C., USA.

449   Karhu, A.A. 1999. A new genus and species of the family Jungornithidae (Apodiformes) from

450   the Late Eocene of the Northern Caucusus, with comments on the ancestry of

451   hummingbirds. Pages 207-216 *in* Olson, S.L., P. Wellnhofer, C. Mourer-Chauviré, D.W.

452   Steadman, and L.D. Martin. Avian Paleontology at the Close of the 20th Century:

453   Proceedings of the 4th International Meeting of the Society of Avian Paleontology and

454   Evolution, Washington, D.C, 4-7 June 1996. Smithsonian Contributions to Paleobiology

455   **89** Smithsonian Institution Press, Washinton, D.C., USA

456   Kaufman, D.M. 1977. Diversity of New World mammals: universality of the latitudinal gradients

457   of species and bauplans. Journal of Mammalogy **76**:322-334

458   Kotler, B. and W.A. Mitchell. 1995. The effect of costly information in diet choice. Evolutionary

459   Ecology **9**:18-29

460   Lima, S.L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a

461   survey of North American birds. The Wilson Bulletin **105**:1-47

462   Mares, M.A. 1975. South American mammal zoogeography: evidence from convergent evolution

463   in desert rodents. Proceedings of the National Academy of Sciences **72**:1702-1706

464   McGhee, Jr., G.R. 1981. Evolutionary replacement of ecological equivalents in late Denovian

465   benthic marine communities. Paleogeography, Paleoclimatology, Paleoecology **34**:267-

466   283

467   McGuire, J.A., C.C. Witt, J.V. Remsen Jr., A. Corl, D.L. Rabosky, D.L. Altshuler, and R. Dudley.

468   2014. Molecular phylogenetics and the diversification of hummingbirds. Current Biology

469   **24**:910-916

470   Mooney, H.A. and E.L. Dunn. 1970. Convergent evolution of Mediterranean-climate evergreen

471   sclerophyll shrubs. Evolution **24**:292-303

472   Montgomery, W.I. 1989. *Peromyscus* and *Apodemus*: patterns of similarity in ecological

473   equivalents. Pages 293-366 *in* Kirkland, G.L. Jr. and J.N. Layne, editors. Advances in the

474   study of *Peromyscus* (Rodentia). Texas Tech University Press, Lubbock, Texas, USA

475   Morhardt, J.E. 1970. Body temperatures of white-footed mice *(Peromyscus* sp.) during daily

476   torpor. Comparative Biochemistry and Physiology **33**:423-439

477   Parslew, B. 2015. Predicting power-optimal kinematics of avian wings. Journal of the Royal

478   Society Interface **12**: 20140953

479   Paton, D.C. and B.G. Collins. 1989. Bills and tongues of nectar-feeding birds: a review of

480   morphology, function and performance, with intercontinental comparisons. Australian

481   Journal of Ecology **14**:473-506

482   Pyke, G.H. 1981. Why hummingbirds hover and honeyeaters perch. Animal Behaviour **29**:861-

483   867

484   Rico-Guevera, A. and M.A. Rubega. 2011. The hummingbird tongue is a fluid trap, not a

485   capillary tube. Proceedings of the National Academy of Sciences **108**:9356-9360

486   Rico-Guevera, A., T. Fan, and M.A. Rubega. 2014. Hummingbird tongues are elastic

487   micropumps. Proceedings of the Royal Society, B **282**:20151014

488 Ros, I.G., L.C. Bassman, M.A. Badger, A.N. Pierson, and A.A. Biewener. 2011. Pigeons steer

489   like helicopters and generate down- and upstroke lift during low speed turns. Proceedings

490   of the National Academy of Sciences **108**:19990-19995

491 Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press,

492   Cambridge, UK.

493 Rosenzweig, M.L. and R.D. McCord. 1991. Incumbent replacement: evidence for long-term

494   evolutionary progress. Paleobiology **17**:202-213

495 Sánchez-Cordero, V. 2001. Elevation gradients of diversity for rodents and bats in Oaxaca,

496   Mexico. Global Ecology and Biogeography **10**:63-76

497 Sanders, N.J. 2002. Elevational gradients in ant species richness: area, geometry, and Rapaport's

498   rule. Ecography **25**:25-32

499 Schlamowitz, R., F.R. Hainsworth, and L.L. Wolf. 1976. On the tongues of sunbirds. The Condor

500   **78**:104-107

501 Schuchmann, K.L. 1999. Family Trochilidae (Hummingbirds). Pages 468-535 *in* J. del Hoyo, A.

502   Elliot, and J. Sargatal, editors. Handbook of the Birds of the World, Vol.5. Lynx Edicions,

503   Barcelona, Spain.

504 Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. Ecology **58**:1007-

505   1019

506 Videler, J.J. 2006. Avian Flight. Oxford Ornithology Series **14** Oxford University Press, Oxford,

507   UK

508 Vincent, T.L. and J.S. Brown. 2005. Evolutionary Game Theory, Natural Selection and

509   Darwinian Dynamics. Cambridge University Press, Cambridge, UK

510   Walton, J.B. and J.F. Andrews. 1981. Torpor induced by food deprivation in the Wood mouse

511   Apodemus sylvaticus. Notes from the Mammal Society **42**:260-263

512   Warrick, D., T. Hedrick, M.J. Fernández, B. Toblaske, and A. Biewener. 2012. Hummingbird

513   flight. Current Biology **22**:R472-R477

514   Wolf, L.L. and F.R. Hainsworth. 1983. Economics of foraging strategies in sunbirds and

515   hummingbirds. Pages 223-264 *in* Behavioral energetics: the cost of survival in

516   vertebrates. W.P. Aspey and S.I. Lustick. Ohio State University Press, Columbus, Ohio,

517   USA

518   Yanega, G.M. and M.A. Rubega. 2004. Feeding mechanisms: hummingbird jaw bends to aid

519   insect capture. Nature **428**:615

520   Zusi, R.L. 2013. Introduction to the skeleton of hummingbirds (Aves:Apodiformes, Trochilidae)

521   in function and phylogenetic contests. Ornithological Monographs **77**:1-94

522   Table 1a: Proportional species richness per elevation interval of sunbirds and hummingbirds

Elevation (meters)	Sunbirds	Hummingbirds
[0 , 500]	0.967741935	0.883040936
(500 , 1000]	1	1
(1000 , 1500]	0.924731183	0.947368421
(1500 , 2000]	0.677419355	0.760233918
(2000 , 2500]	0.376344086	0.543859649
(2500 , 3000]	0.172043011	0.421052632
(3000 , 3500]	0.107526882	0.292397661
(3500 , 4000]	0.053763441	0.140350877
(4000 , 4500]	0.043010753	0.058479532
(4500 , 5000]	0.021505376	0.005847953

523

524   Table 1b: Proportional species richness per latitudinal interval of sunbirds and hummingbirds

Latitude (degrees)	Sunbirds	Hummingbirds
[0 , 5]	0.904761905	0.76953125
(5 , 10]	1	1
(10 , 15]	0.80952381	0.86328125
(15 , 20]	0.495238095	0.6953125
(20 , 25]	0.380952381	0.37109375
(25 , 30]	0.314285714	0.25
(30 , 35]	0.2	0.15234375
(35 , 40]	0.00952381	0.05859375
(40 , 45]	0	0.03515625
(45 , 50]	0	0.02734375
(50 , 55]	0	0.0234375
(55 , 60]	0	0.01171875
(60 , 65]	0	0.00390625

525

526   Table 2: The results of the ECDF comparisons between families. *Italics* indicate the centrality

527   based ECDFs. **KS** stands for Kolmogorov-Smirnov and **AD** stands for Anderson-Darling. NS

528   indicates that the result was non-significant.

ECDF Type	Hbird Num	Sbird Num	KS D-statistic	KS Significance	Standardized AD Criterion	AD Significance
Minimum Elevation	309	119	0.331783199	p<0.001	31.482	p<0.001
Maximum Elevation	309	119	0.163280846	p<0.05	3.2666	p<0.01
Midpoint Elevation	309	119	0.214598461	p<0.001	8.685	p<0.001
Minimum Latitude	365	124	0.234423332	p<0.001	10.207	p<0.001
Maximum Latitude	365	124	0.069443217	NS	0.49404	NS
Midpoint Latitude	365	124	0.156407424	p<0.05	1.7652	p<0.05
Minimum Polewardness	365	124	0.242222713	p<0.001	14.455	p<0.001
Maximum Polewardness	365	124	0.073486522	NS	0.71488	p<0.1
Midpoint Polewardness	365	124	0.14719399	p<0.05	1.4571	p<0.05
Expected Polewardness	365	124	0.13121962	p<0.05	1.8851	p<0.05

529

530   Table 3: The values of a and b for each of the models along with their significance. RSS is the

531   residual sum of squares for each model and RSE is the residual standard error. It should be noted

532   that all residuals fall between 0 and 1, and therefore the sum of squares are smaller than the sum

533   of the absolute values of the residuals.

Model	a	b	RSS	RSE
NectarElev	0.00655[d]	2.40963[a]	0.010254	0.035802
TrochElev	0.02024[c]	1.53943[a]	0.022979	0.053594
NectarLat	0.04133[c]	0.15735[a]	0.04463	0.063696
TrochLat	0.02318	0.17739[a]	0.054938	0.070671

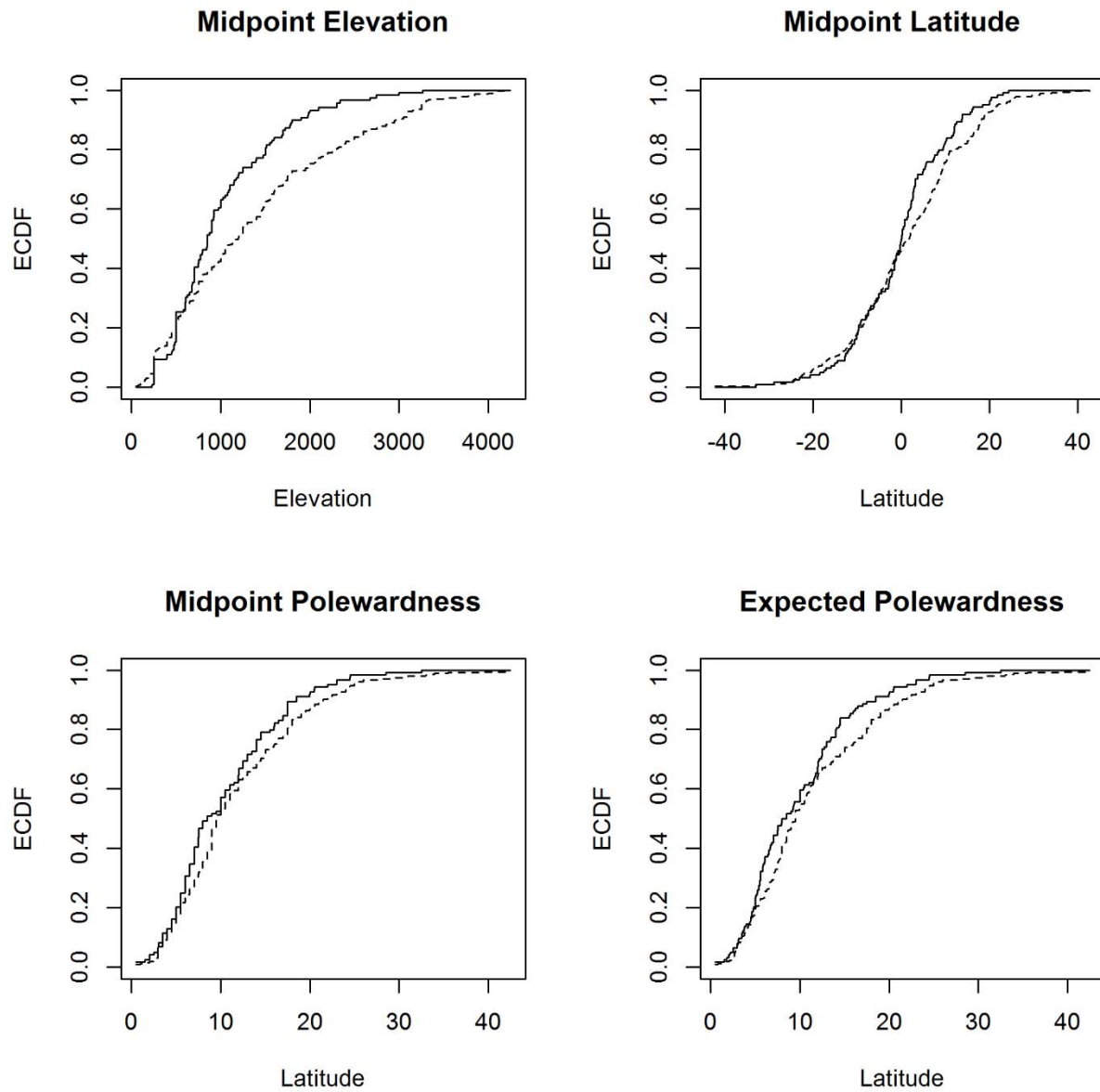534   _a: p<0.001, b: p<0.01, c: p<0.05, d: p<0.1

535   Table 4: The Inflection point, the jerk points, and MMC points for each of the models.

Model	Inflection	Jerk #1	Jerk #2	Curve #1	Curve #2
NectarElev	2.087005	1.540442	2.633544	1.441369	2.73264
TrochElev	2.533536	1.678043	3.389003	1.608667	3.458399
NectarLat	20.24934	11.87956	28.61911	11.872	28.62667
TrochLat	21.22319	13.7989	28.64747	13.79037	28.656

536

537   Fig. 1 A plot of the four main ECDFs used to compare hummingbird and sunbird distribution.

538   Solid lines indicated the sunbirds and dashed lines indicate hummingbirds. One can see that the

539   hummingbird ECDFs are almost entirely below and reach the 1 at much a higher latitude and

540   elevation compared to the sunbird ECDFs. One can also see that the deviation between the

541   elevation-based ECDF is significantly larger than the deviations of the latitudinal based ECDFs.

542   Fig. 2 A plot of the proportional species richness S_p of hummingbirds and sunbirds, along with

543   the fitted line, for elevation (a,c) and latitude (b,d). Hummingbirds are denoted by the triangles

544   and dashed lines while sunbirds are denoted by the circles and solid lines. One can see that

545   hummingbirds sustain their species richness at higher elevations and mid-latitudinal ranges, and

546   extend farther latitudinally than sunbirds. The calculated inflection (non-diagonal cross), jerk

547   (diagonal cross), and MMC points (asterisks) also are shown for elevation (c) and latitude (d). As

548   seen in the figures inflection points come later in hummingbirds than sunbirds, confirming that

549   hummingbirds hold up better than sunbirds. We also see that hummingbird S_p and sunbird S_p

550   start their elevational decline at the same spot but eventually separate by the end of the decline,

551   while with latitude, sunbird S_p declines earlier but hummingbird S_p quickly declines until the

552   declines end at roughly the same point.

553   Fig. 1

554

555   Fig. 2

556