

Wings of tropical finches

Interspecific differences in shape are consistent with levels of mobility, but moult and feather fault patterns are more complex

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1 **Wings of tropical finches: interspecific differences in shape are consistent with levels of**
2 **mobility, but moult and feather fault patterns are more complex**

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51 **Wings of tropical finches: interspecific differences in shape are consistent with levels of**
52 **mobility, but moult and feather fault patterns are more complex**

53

54 **Abstract**

55

56 Birds' wings reflect their life histories, suggesting evolutionary selection for wing shapes and
57 moult strategies. Compared to sedentary species, long-distance migrants have narrower wings
58 (for fast, efficient flight); they have fewer feather faults and avoid moulting flight feathers
59 during migration (to optimise flight surface performance). It is unclear whether these patterns
60 apply to species that fly short-intermediate distances, like tropical nomads. We compared
61 wing shape, feather faulting, and flight feather moult across five finch species from northern
62 Australia with varying mobility: Pictorella Mannikins *Heteromunia pectoralis* and Gouldian
63 Finches *Erythrura gouldiae* are highly mobile, nomadic at regional scales; Long-tailed
64 Finches *Poephila acuticauda* and Double-barred Finches *Taeniopygia bichenovii* are
65 sedentary with local nomadism; Crimson Finches *Neochmia phaeton* are sedentary. More
66 mobile species had narrower wings and higher wing loading than relatively sedentary species,
67 and less feather faulting. Variation in moult strategies was complex, but mobile species
68 carried out moult fast, in a short time window, and moulted a single feather at a time.
69 Unexpectedly, Gouldian Finch wings were more suited for fast efficient flight than Pictorella
70 Mannikin wings, and yet they had more feather faulting. Differences in mobility may be a
71 key dimension of niche separation that allows these species to co-exist.

72

73 Key words: feather fault, wing shape, moult strategy, Gouldian finch, nomadic bird, tropical
74 savanna

75

76 Word Count: 7260 (Abstract to refs)

77 **Introduction**

78

79 To minimise the energetic demands of long-distance flight, the wings of migratory birds have
80 a higher aspect ratio (i.e. are longer and narrower) and are more pointed and convex than less
81 mobile relatives (Lockwood et al. 1998; Mila et al. 2008; Baldwin et al. 2010). High aspect
82 ratios reduce the mechanical power needed for flight (Norberg 2013). The wing loading
83 (weight per unit wing area) of migrants is variable, and depends on how fast they need to fly:
84 combined with a high aspect ratio, low wing loading reduces the power needed to fly, but
85 also reduces the flight speed. Fast-flying migrants may therefore combine a high aspect ratio
86 with a relatively high wing loading (Norberg 2013). Migratory birds also moult more rapidly
87 (Kjellen 1994; de la Hera et al. 2009) and avoid moulting during migration (Podlaszczuk et
88 al. 2016), in order to avoid compromising the flight surfaces and reducing flight performance
89 (Navarro and Gonzalez-Solis 2007).

90

91 Migrants may also allocate relatively more resources to growing primary feathers in the wing
92 than the tail (de la Hera et al. 2010) to reduce the likelihood of faults and breakages in the
93 primary feather vane (Møller et al. 2009). Feather faults, which usually appear as transparent
94 lines across the vane, originate when the feather is growing due to a structural abnormality in
95 the formation of barbules. They arise as a result of a variety of stressors including poor
96 nutrition and disease (Jovani and Blas 2004; Jovani et al. 2010; Jovani and Rohwer 2016).
97 Faults weaken the feather, and if they develop into a breakage (where part of the vane is lost),
98 the reduced feather surface area can affect flight performance and individual fitness
99 (Bortolotti et al. 2002; Eggers and Low 2014). The incidence and location of faults bars is
100 thus subject to natural selection (Jovani and Rohwer 2016) and faults are usually rarer on
101 individual feathers that are critical for flight, like primaries, and also rarer in highly mobile
102 species, such as long-distance migrants (Serrano and Jovani 2005; Sarasola and Jovani 2006;
103 Møller et al. 2009; Jovani et al. 2010; Jovani and Rohwer 2016).

104

105 Several studies suggest that locally-migratory or nomadic species are subject to similar
106 selective pressures on wing morphology and moult patterns as long distance migrants, albeit
107 to a lesser degree. For example wheatears (*Oenanthe* spp.) occupying arid regions have more
108 pointed wings than those of less-arid regions, plausibly because birds in arid regions have to
109 track sparse food resources at greater spatial scales; however, they had less-pointed wings
110 than congeners that migrate long distances (Kaboli et al. 2007). Similarly, within the warbler

111 family, moult strategy varied with migration distance (Hall and Tullberg 2004). In a broader
112 comparative review, De la Hera et al. (2009) found that the time taken to complete moult in
113 short-distance migrants was intermediate between that of sedentary species and long-distance
114 migrants. Finally, Silvereyes (*Zosterops lateralis*) from a partially-migratory population in
115 Australia commence moult earlier and on a more fixed schedule than members of a sedentary
116 population of the same species (Munro et al. 2006). These trends have mostly been identified
117 from high-latitude regions. Trends may differ in tropical areas as they provide a longer
118 season that is suitable for moult and breeding. Furthermore, tropical nomads may have less
119 rigid annual schedules than higher latitude species, and their need to move is less predictable;
120 this may render some overlap between moult, breeding and major movements unavoidable in
121 tropical areas.

122

123 Relative mobility may be a key dimension of niche separation that allows granivorous species
124 to co-exist in some areas. Granivorous birds track variability in seed production and soil seed
125 banks through time and space (Price and Joyner 1997; Dostine et al. 2001), but the spatial
126 scale at which they do so varies among species (Blendinger and Ojeda 2001; Siriwardena et
127 al. 2006). Resource generalist granivores may survive in a relatively small area (e.g. often <
128 10 ha for finches, Brandt and Cresswell 2008), foraging on a wide range of seed types and
129 even exploiting non-seed resources when seeds are scarce (Dostine and Franklin 2002). In
130 contrast, resource specialists may exhibit great mobility, tracking rich seed patches (Brown et
131 al. 1994; Areta et al. 2009). Garb et al. (2000) and Soobramoney and Perrin (2008)
132 demonstrated that sympatric species may vary in “giving-up density” responses to seed
133 supply, implying interspecific variation in willingness or ability to seek better alternatives as
134 local food supplies diminish.

135

136 Niche separation along a spectrum of levels of mobility may partly explain the co-existence
137 of 11 sympatric species of grass-finch in the tropical savannas of the Kimberley region of
138 north-western Australia. They range in mass from 7.5 – 15 g, but display little morphological
139 variation in bill types (Higgins et al. 2006). Their feeding behaviour is similar; they eat grass-
140 seed, usually from the ground but also from standing grass stalks (in the wet season). There is
141 some separation of species by habitat, but mixed-species flocks are a common seasonal
142 occurrence. Despite these ecological similarities, there is marked interspecific variation
143 amongst finches in their sensitivity to contemporary land use changes. Variation in mobility
144 may also relate to this, because changed fire regimes and grazing by introduced herbivores

145 have modified the spatio-temporal availability of grass seed (Maute et al. 2013; Legge et al.
146 2015).

147

148 In this study, we compare and contrast the wing morphology (wing loading, aspect ratio),
149 flight feather fault patterns and moult strategies of five sympatric finch species (Estrildidae)
150 from the tropical Kimberley region of northern Australia (Table 1). These species vary in
151 mobility, from occupying small home ranges throughout the year to being nomadic at scales
152 of tens or even hundreds of kilometres (reviewed below). If the physical implications of
153 resource-tracking at contrasting spatial scales provide a unifying set of selective forces in
154 these finches, then we anticipate a positive association between mobility, wing loading and
155 aspect ratios (to allow fast and energy-efficient flight; Norberg 2013); a negative association
156 between mobility and the incidence of feather faults; and that more mobile species will
157 reduce gaps in the flight surface of their wings by rapidly moulting one feather at a time
158 (Pennycuik 1975).

159

160 **Methods**

161

162 *Study area and species*

163

164 Our study was conducted at Mornington Wildlife Sanctuary (17°30'S, 126°07'E), a 3,210
165 km² conservation reserve in the central Kimberley region of northern Western Australia,
166 managed by the Australian Wildlife Conservancy (<http://www.australianwildlife.org/>). The
167 climate is monsoonal tropical, with a mean annual rainfall of c. 750 mm. Temperatures are
168 high throughout the year. The predominant vegetation types are semi-arid lowland savanna
169 (grassland with scattered trees including *Eucalyptus* spp., *Corymbia* spp., *Bauhinia*
170 *cunninghamii* and *Adansonia gregorii*, and sandstone hills and escarpments with spinifex
171 hummock grasses (*Triodia* spp.). The Sanctuary has a number of permanent and semi-
172 permanent watercourses including the Fitzroy, Hann and Adcock Rivers which support
173 narrow bands of riparian forest; the sandstone areas also feature many permanent waterholes.

174

175 Australian finches have nine primaries and eight secondaries (including three tertials) per
176 wing, and 12 rectrices (tail feathers) (Higgins et al. 2006). Primary moult is descendant (from
177 the inside out). Adults of the study species undertake a complete annual pre-basic moult.
178 There is no pre-alternate moult (no moult into a distinct breeding plumage). Juveniles of all

179 our study species moult directly into adult plumage. With the exception of the Gouldian
180 Finch, juvenile plumage of our study species differs from adult plumage only by degrees and
181 often subtly, and no species can be readily aged by its flight feathers. Full adult body
182 plumage is usually gained within two to nine months of hatching, the period being longest in
183 the Gouldian Finch *Erythrura gouldiae* and Pictorella Mannikin *Heteromunia pectoralis*
184 (Higgins et al. 2006). The post-juvenile moult is complete or believed to be complete in three
185 species, but not in Gouldian or Crimson Finches *Neochmia phaeton* (Franklin et al. 1998;
186 Milenkaya et al. 2011).

187

188 TABLE 1 near here

189

190 Crimson Finches and Double-barred Finches *Taeniopygia bichenovii* mostly forage close to
191 waterholes during the dry season, whilst Long-tailed Finches *Poephila acuticauda* and
192 especially Gouldian Finches and Pictorella Mannikins range much more widely on a daily
193 basis (Evans et al. 1985; SL and DCF pers. obs.). Radio-tracked Gouldian Finches have been
194 recorded moving over 10 km in a day (Palmer 2005; SL pers. obs.). On a seasonal basis, the
195 distances over which species track resources is not well documented – the best information
196 comes from Gouldian Finches, which use contrasting components of the landscape that may
197 be separated by a few to very many kilometres in the course of a year (Dostine et al. 2001).
198 Among-years, banding studies show high recapture rates for Crimson, Double-barred and
199 Long-tailed Finches, and low to exceptionally low recapture rates for Gouldian Finches and
200 Pictorella Mannikins (Woinarski and Tidemann 1992; van Rooij and Griffith 2011; SL and
201 DCF pers. obs.). Pictorella Mannikins are particularly irruptive, at times appearing in areas
202 hundreds of kilometres beyond their normal range (Ley and Tynan 2011) while Gouldian
203 Finches do so occasionally. All five species co-occur in the same habitat (open savannah),
204 though they show a preference for some components of that habitat (e.g. Crimson Finches are
205 nearly always within a kilometre of a watercourse). They all feed predominantly on grass
206 seed, mostly by dropping onto the ground. During the wet season, birds occasionally collect
207 seed directly off a plant stem. The Gouldian Finch is demonstrably a rich-patch specialist,
208 consuming larger seeds of less variety than other finches (Dostine and Franklin 2002). We
209 interpret this evidence as representing a hierarchy of mobility in the order Pictorella
210 Mannikin > Gouldian Finch > Long-tailed Finch > Double-barred Finch > Crimson Finch.

211

212 ***Field data***

213

214 The study was carried out between June 2004 and September 2012. Birds were caught using
215 mist nets and walk-in traps, sometimes aided by call-playback, set at waterholes and feeding
216 sites. Most captures were made within two hours of dawn, but trapping efforts were
217 sometimes extended during cooler weather conditions. Nets and traps were attended
218 continuously, and birds removed and placed in soft cotton bags almost immediately after
219 capture. Over the eight years of the study, moult data were collected by 22 licenced bird
220 banders; one bander (SL) determined the specific moult information to be collected from
221 each bird and oversaw other banders' assessments to ensure that moult data were recorded
222 consistently. SL also trained other banders to carry out the wing tracings as consistently as
223 possible.

224

225 Birds were banded with individually-numbered metal bands and weighed with a pesola
226 balance (+/- 0.5 g). Birds were aged (juvenile/adult) based on plumage colour and the status
227 of nodules around the beak; gender was identified for those species with clear gender-specific
228 plumage characteristics (i.e. Crimson Finches, Gouldian Finches, Pictorella Mannikins). The
229 amount of additional data collected depended on catch rates and temperature (finches may be
230 caught in large numbers and need to be released quickly in hot weather, precluding collection
231 of the full suite of measurements), other research priorities (e.g. collection of blood samples
232 versus morphometric measurements), and the experience of the assessor (which affects how
233 quickly data are collected).

234

235 Traces of the right wing were made for a sample of birds by extending the wing over a flat
236 piece of card, butted up against the bird's armpit, then tracing the outline of the wing onto the
237 card in pencil. The bird (and its wing) was held in a consistent manner to reduce variation
238 among observers.

239

240 The minimum data to be useful for the analysis of moult was the presence or absence of
241 growing feathers in the primary tract. This was frequently extended to include the
242 presence/absence of growing feathers in the secondaries (including tertials) and tail, and to
243 the recording of full moult scores in the primaries or all flight feather tracts using standard
244 protocols (Ginn and Melville 1983; Lowe 1989) as: 0 = old; 1 = missing or pin only; 2 = <
245 1/3 grown; 3 = 1/3 to < 2/3 grown; 4 = 2/3 to fully grown but with a waxy sheath; and 5 =

246 fully developed new feather. Moulting scores were recorded directly on to a standard diagram of
247 a bird showing each flight feather.

248

249 During capture, the nine primaries, eight secondaries and six tail feathers on the left side of
250 each bird were scored for the number of faults. Faults included incomplete fault bars (a fault
251 that partially extends across the feather), complete fault bars (faults that extend across the
252 entire plain of the feather), partial breakages (breaks that partially extend across a feather),
253 and complete breakages (when the feather is broken off). We only scored faults in feathers
254 that were >75% grown and only included data from the first time a bird was captured.

255

256 ***Data analysis***

257

258 To further ensure consistency in wing traces, we used traces from only six experienced bird
259 handlers who each made large numbers of tracings. Traces were further assessed for quality,
260 including appropriate extension of the wing and proper placement of the card firmly under
261 the armpit. Wing tracings were made of 238 birds; we used 73 of the best quality tracings in
262 analysis (between 10-22 per species, Table 1). Wing traces were scanned electronically, wing
263 length and wing area measured as pixel counts, and these transformed back to conventional
264 measurements. The wing tracing was doubled to give the total wing area. Wing loading is the
265 bird mass divided by the total wing area. Aspect ratio was calculated as:

266

$$267 \quad AR = ((2 * WL)^2) / (2 * WA)$$

268

269 where AR = Aspect ratio, WL = Wing length and WA = Wing area. WL and WA were
270 doubled because measurements were for one wing only.

271

272 Wing loading and aspect ratio were compared among species using conventional one-factor
273 ANOVAs. They were also compared in multivariate space (analogous to a MANOVA) using
274 permutational ANOVA in the PERMANOVA+ add-on to PRIMER v6 (Anderson et al.
275 2008).

276

277 To identify seasonal patterns of moulting and breeding, we combined data across years. This
278 approach is justifiable *as a first approximation* because of the reliable seasonality of rainfall
279 in the monsoon tropics (e.g. McDonald and McAlpine 1991; Suppiah 1992; Zhang and Wang

280 2008) and the distinctly seasonal responses of north Australian finches to it (e.g. Tidemann et
281 al. 1999; Dostine et al. 2001; Todd 2002; Lewis 2007; Legge et al 2015; see also Woinarski
282 et al. 2005).

283

284 To provide an indication of the timing of breeding activity, we calculated the percentage of
285 the catch that were juveniles for each month. An increase in the percentage from one month
286 to the next suggests that breeding occurred in the previous month (incubation and nestling
287 period combined is usually 27–39 days for these species; Higgins et al. 2006). A decrease
288 does not preclude the possibility of breeding, but suggests that the number of young produced
289 was less than the combined effects of mortality, emigration and the moult of juveniles into
290 adult plumage.

291

292 In analysing moult data, we sought measures that were robust across assessors. We have
293 defined moult activity in the set of primaries on a wing as the presence of one or more
294 feathers that were missing or growing or new with a waxy sheath (score 1 to 4 as above).
295 Whilst some birds may have been between growing a feather and shedding the next and thus
296 be misclassified as not in moult, such individuals may also be in a state of arrested moult and
297 thus correctly classified as not in active moult. This definition also precludes the necessity to
298 distinguish between new and old feathers, a distinction that is often unclear in finches,
299 especially juveniles where the “old” flight feathers may be as little as a few months old
300 (Franklin et al. 1998).

301

302 To develop primary moult wing scores we assumed that feathers inwards from growing
303 feathers were new (i.e. primary moult is descendent) and attributed to them a score of 5,
304 resulting in wing scores summed across all primary feathers ranged from 1 to 44. The time
305 taken to complete primary moult was determined from rates identified for *prima facie* within-
306 moult recaptures, and assuming linear progression of moult scores. Assuming linearity is not
307 ideal (Dawson and Newton 2004), but acceptable for most passerines in which the relative
308 length of the primary feathers does not vary greatly (Ginn and Melville 1983). To avoid the
309 potential for noise associated with short intervals, we only used recaptures that were > 15
310 days apart.

311

312 We analysed the incidence of feather faults among species. To do this, we needed to account
313 for differences in faulting between feather types (because tail feathers usually have more

314 faults than secondaries, which have more faults than primaries; (Jovani and Blas 2004; Jovani
315 et al 2010), and we needed to account for differences in the age of feathers. New feathers are
316 expected to have faults but rarely breakage; the incidence of breakages (which mostly occur
317 at original fault lines) is expected to change non-linearly throughout the year as ageing
318 feathers increasingly develop breaks until the feathers are replaced during the moult. Feather
319 breakages are easier to see (and thus record) than fault lines, which will tend to bias the
320 recorded incidence of feather faults between freshly moulted feathers and older feathers.
321 Using R 3.1.1 (The R Foundation for Statistical Computing), we characterized these patterns
322 using a generalized additive mixed modelling framework (GAMM) which extends
323 generalized linear models to include smoothed functions of explanatory variables that are not
324 linear (in this case, Month, as an approximation of feather age, was fitted with a smooth
325 function). We used the gamm4 function fit by maximum likelihood (Wood and Scheipl
326 2014), to characterize whether incidence of feather faults differed with species, feather type
327 (primary, secondary, tail), bird age (adult, juvenile), and feather age (Month). The number of
328 feathers differs between feather types; we used a ratio as the response variable (building on
329 Serrano and Jovani 2005), where the number of feathers with faults for each feather type
330 (primary, secondary, tail) was the numerator, and the number of feathers without faults for
331 each feather type was the binomial denominator, per individual. The model was weighted by
332 the total number of feathers sampled per feather type per individual. The individual finch was
333 specified as a random intercept. We used a binomial error distribution with logit link
334 function. We evaluated the goodness-of-fit of the model by conducting a log-likelihood ratio-
335 test comparing the model described above, with a null model with intercept of 1.

336

337 **Results**

338

339 *Wing morphology*

340

341 Rank ordering of finch species according to wing loading and aspect ratio were identical,
342 Gouldian Finches having the highest values and Crimson Finches the lowest of both
343 measures (Fig. 1). Considered both as individual attributes and as points in multi-variate
344 space, the five finch species differed with respect to both measures (wing loading, $F_{4,68} =$
345 31.5 , $P < 0.0001$; aspect ratio, $F_{4,68} = 65.4$, $P < 0.0001$; in multivariate space, pseudo- $F_{4,68} =$
346 53.5 , $P = 0.0001$). Post-hoc comparisons of position in multivariate space demonstrated that

347 all species-pairs were separable ($P < 0.01$) except Pictorella Mannikin and Long-tailed Finch
348 ($P = 0.20$).

349

350 FIGURE 1 near here

351

352 *Moult patterns*

353

354 For four finch species netted in all months, the percentage of the netted population that were
355 juveniles increased in all four species from the late wet season (c. March) to the mid dry
356 season (c. July) (Fig. 2), describing the timing of fledging. However, the increase was
357 markedly more abrupt in the Gouldian Finch than the other species, occurring predominantly
358 in May. Declines in the percentage occurred in the second half of the year and may represent
359 mortality as well as the transition of birds to adult plumage. Although our data do not
360 preclude the possibility of young fledging later in the year, clearly numbers were low and
361 insufficient to compensate for the attrition. However, since juvenile Double-barred Finches
362 rapidly become indistinguishable from adults, it seems likely that this species breeds
363 throughout the dry season because juveniles were recorded in every month except January.

364

365 FIGURE 2 near here

366

367 Molt had different seasonal patterns across the finch species. Double-barred Finches and
368 Long-tailed Finches were recorded moulting throughout the year: more than 20% of the adult
369 populations of both species were actively growing primary feathers in most months of the
370 year, but with seasonal peaks of 50 to 80% later in the year after the main fledging period
371 (Fig. 2). In contrast, adult Gouldian Finches undertook primary moult that was synchronised
372 across the population, so that moulting was detected over a very short period late in the dry
373 season (August – October), after the main fledging period. Crimson Finches showed an
374 intermediate pattern: moult was detected over most of the year, but the primary moult was
375 concentrated between May to July.

376

377 Molt of secondaries (and to a lesser extent tail feathers) in adult Crimson, Double-barred
378 and Long-tailed Finches loosely followed primary moult with a delay of up to several months
379 (Fig. 2). In the Gouldian Finch, however, moult of secondaries and tail feathers was strongly

380 coincident with that of primary moult, accentuating the population-level synchronicity of
381 moult.

382

383 In the Crimson Finch, post-juvenile moult generally occurred 1–2 months after that of adults,
384 peaking in July and August. In the Gouldian Finch, post-juvenile moult commenced at the
385 same time as that of adults but continued into the early wet season (Nov. – Dec.). As with
386 adults, juveniles of the Long-tailed Finch were recorded in moult throughout the year but
387 with a peak in the second half. Given the difficulty of aging Double-barred Finches, we were
388 unable to distinguish post-juvenile moult from adult moult.

389

390 Of the months with >10 captures of the Pictorella Mannikin (Sept. to Feb.), the percentage of
391 the catch that were juveniles ranged from 40 to 68% in Sept., Oct. and December and was
392 zero in Jan. and Feb. The 26 juveniles and 21 adults recorded growing new primary feathers
393 were all captured in Sept., Oct. and Dec., with mid- to late-stage primary moult in October.
394 These observations suggest Pictorella Mannikins moult after the main nesting period, and that
395 moult occurs within a short window.

396

397 *The nature of primary moult*

398

399 Based on the few individuals recaptured and scored for primary moult during the one moult
400 sequence, with juveniles and adults necessarily pooled because of small samples, Long-tailed
401 Finches took 40–50% longer to complete primary moult than Crimson or Gouldian Finches,
402 although this difference was not significant, and variation among Long-tailed Finches was
403 particularly marked (Table 2; ANOVA comparison of three species: $F_{2,19} = 2.89$, $P = 0.080$).

404

405 TABLE 2 near here

406

407 The number of feathers growing at once varied among both species and age classes (Table 3),
408 with a highly significant interaction indicating that the difference between age classes was
409 not consistent among species (Log-linear model (two and three feathers combined into a
410 single class, and Pictorella Mannikin excluded due to small sample size): species – $\chi^2_3 =$
411 310.3, $P < 0.0001$; age – $\chi^2_1 = 278.6$, $P < 0.0001$; species x age, $\chi^2_3 = 256.5$, $P < 0.0001$).

412

413 Adult Crimson Finches most commonly had more than one primary feather per wing growing
414 at a time, whereas in all other species x age class combinations, the modal category was a
415 single feather. Differences between adults and juveniles were significant for the Crimson
416 Finch (two-tailed Fishers Exact Test, $P = 0.0001$) and Gouldian Finch (two-tailed Fishers
417 Exact test, $P = 0.048$), but not in the Long-tailed Finch (Yates-corrected Chi-square, $P_1 =$
418 0.69) notwithstanding a very large sample size in the latter. In the former two species, adults
419 were more likely to be growing more than one feather at once than were juveniles (Table 3).
420 The sample of juveniles in Double-barred Finches was too small to test adequately for age-
421 related differences, but the frequency of adults with two or more feathers growing was
422 similar to Crimson and Gouldian Finches.

423

424 TABLE 3 near here

425

426 Where an individual was growing more than one primary feather in a wing simultaneously,
427 this effect may be partitioned into adjacent feathers and multiple waves. Amongst adults,
428 there were significant differences between species in the number of waves present in a wing,
429 with the Double-barred Finch commonly moulting in two or more waves and the Crimson
430 Finch rarely so (i.e. multiple growing feathers were mostly adjacent) (Table 4; Log-linear
431 model for adults (two and three waves combined into a single class): $\chi^2_3 = 8.3$, $P = 0.004$).
432 There were too few data to include juveniles in the statistical model, but the data (Table 4)
433 suggest juvenile Crimson Finches were more likely, and juvenile Gouldian and Long-tailed
434 Finches less likely, than adults to moult in multiple waves.

435

436 Pictorella Mannikins mostly grew one primary feather per wing at a time (Table 3), and the
437 few exceptions involved only a single wave of moult (Table 4).

438

439 TABLE 4 near here

440

441 *Feather faults*

442

443 Faults were quantified in 51,154 feathers sampled from 2,340 finches. A high proportion of
444 feathers sampled were free of faults (89.6%) but 1.4% had incomplete faults, 0.2% had
445 complete faults, 8.9% had incomplete breaks and 0.7% had complete breaks. For those
446 feathers with faults, the majority had only one (68.7%) or two faults (18.9%). 1.5% of

447 feathers with damage had more than six faults, with the maximum number being twenty per
448 feather ($n = 1$). All feathers with more than six faults were tail feathers. Faults were not
449 distributed evenly among feather types. Only 4% of primaries and 5% of secondaries had
450 some form of faulting, compared to 27% of tail feathers.

451

452 The full GAMM captured more of the deviance in the incidence of feather faulting than a null
453 model (delta deviance 5019; $\chi^2_9 = 5019.1$, $P < 0.001$). As expected, feather faulting was more
454 evident closer to moulting; in addition, primaries had fewer faults than secondaries, and both
455 had much fewer faults than tail feathers (Table 5). Age did not affect the incidence of feather
456 faults (Table 5). After controlling for the influence of feather type and month, Crimson
457 Finches had the highest incidence of feathers faulting, followed by Long-tailed Finches and
458 Double-barred Finches. Gouldian Finches had feather faults at a marginally lower rate than
459 these three species. Pictorella Mannikins were the least likely to have feather faults (Table 5;
460 Fig. 3).

461

462 TABLE 5 near here

463

464 **Discussion**

465

466 Our findings are broadly consistent with the notion that finch species have wing
467 morphologies and feather fault patterns that reflect their level of daily and seasonal mobility,
468 but patterns of flight-feather moult are less obviously consistent with this hypothesis (Table
469 6). More mobile species, such as Gouldian Finches, have higher wing loadings and aspect
470 ratios (longer, narrower wings), allowing efficient fast flight. They have fewer feather faults,
471 moult over a short period, and grow just one new primary feather per wing at a time, which
472 would limit adverse effects on flight performance from having gaps in the feather surface. In
473 contrast, and as anticipated, the Crimson and Double-barred Finch display wing
474 morphologies and feather fault patterns consistent with being resident within relatively small
475 home ranges.

476

477 Alternative explanations for the variation in wing morphology, feather faulting and moulting
478 can be discounted. The habitat and foraging ecology of these sympatric finch species are too
479 similar to invoke differences in selective pressures on wing and feather attributes due to
480 differences in foraging habitat or behaviour (e.g. White et al. 2016). The five species vary 1.5

481 fold in body mass, and body mass is related to some of the attributes we measured, but
482 usually in ways opposite to the observed patterns. For example, feather replacement in larger
483 birds takes longer, so they generally take longer to moult; to partially compensate they grow
484 their feathers faster and may moult more than one feather at a time (Rohwer et al. 2009);
485 however, in our study, the larger finches moulted over a shorter period, did not clearly grow
486 feathers faster, and were less likely to moult more than a single feather at a time. Wing
487 loading generally increases allometrically with bird mass, but aspect ratio is independent of
488 body mass in geometrically similar birds (Norberg 2013), so the variation observed cannot be
489 explained by differences in body mass.

490

491 Accepting that differences in mobility are behind the patterns in wing morphology, feather
492 faulting and moult, the few exceptions to these patterns are interesting and potentially
493 informative. For example, the Pictorella Mannikin is less well-adapted to long-distance flight
494 than the Gouldian Finch, mostly because of lower aspect ratios. Considerable variation in the
495 Pictorella Mannikin wing loadings suggest that further data may sharpen this estimate. We
496 are surprised by this result as the Pictorella Mannikin is both demonstrably highly mobile and
497 observably an exceptionally strong-flying finch. Their low feather fault incidence is
498 consistent with reliance on efficient flight, as is the tight seasonality of moult (although this
499 observation is based on a small sample). Speculatively, the Gouldian Finch may be more
500 mobile on a day-to-day basis, travelling further between its specialised nest sites (the species
501 is an obligate hollow-nester; Tidemann et al. 1992; Brazill-Boast et al. 2010) and water and
502 feeding sites, whereas the Pictorella Mannikin is more mobile in tracking food, water and
503 nesting (they nest in grass hummocks) resources on a seasonal or annual basis. The
504 requirements of daily flight may be the greater selective pressure on wing morphology. This
505 proposed difference in mobility patterns is consistent with the finding that individual body
506 condition in Gouldian Finches is especially responsive to changes in fire and grazing
507 management that would affect grass seed availability at relatively local scales (Maute et al.
508 2013; Legge et al. 2015).

509

510 The incidence of feather faults was broadly consistent with our expectations, with Pictorella
511 Mannikins having fewest faults, and Crimson Finches having most. However, the incidence
512 of feather faults in Gouldian Finches was only slightly less than for Double-barred Finches,
513 and Long-tailed Finches had more faults than Double-barred Finches. Although species and
514 feather types may fundamentally differ in their propensity to produce fault bars, the incidence

515 of fault bars can also be modified by stressors experienced by individual birds during their
516 moult (Jovani et al 2016). The surprisingly high fault rates in both the Gouldian and Long-
517 tailed Finches could arise if those species experience stress during their moulting period as a
518 result of contemporary land management practices, as has been suggested elsewhere (Dostine
519 et al. 2001; Dostine and Franklin 2002; Legge et al. 2015; Maute et al. 2015).

520

521 Variation in moult strategies was less clearly aligned with mobility. Despite having wing
522 morphology and feather faulting consistent with intermediate mobility, the Long-tailed Finch
523 population had an extended moult period and slow individual moult rates (consistent with
524 low mobility); a previous study in the Northern Territory also reported an extended moulting
525 season and slower individual moult rates for this species (Tidemann and Woinarski 1994).
526 Wing morphology and high feather faulting patterns suggested that Crimson Finches were
527 less mobile than Double-barred Finches, and yet the latter species had a moult strategy that
528 suggested the opposite: Double-barred Finches were more likely to grow more than one
529 feather at a time, to do so in multiple waves, and to do so more slowly.

530

531 The moulting patterns of Gouldian Finches were particularly interesting. Gouldian Finches
532 delay moult for a number of months after completing nesting (most birds moult soon after
533 breeding, like the Crimson Finch in Fig. 2), individuals moult rapidly and in synchrony
534 across the population shortly before the onset of the wet season. This mirrors observations of
535 moult in Gouldian Finches in the Northern Territory (Tidemann and Woinarski 1994). As
536 noted by Franklin et al. (1998), this suggests a need to complete moult before dispersal
537 associated with germination of grasses early in the wet season, compressing moult into a time
538 of year when food supplies are relatively low and perhaps contributing to seasonal stress that
539 is reflected in relatively high feather faulting (this study) and poor body condition indices at
540 that time of year compared with sympatric finch species (Legge et al. 2015; Maute et al.
541 2015).

542

543 ***Conclusion***

544

545 Whilst wing morphologies and feather fault patterns corresponded with levels of mobility in
546 our five study species, moult strategies were less strongly aligned and presumably reflect
547 additional life history complexities and environmental stressors. The seasonality and rate of
548 moult varied considerably among species with an apparent gradation between relatively

549 rapid, strongly-seasonal moult in Gouldian Finches (and probably *Pictorella* Mannikins),
550 through to the slower and/or less seasonal moult in Long-tailed and especially Double-barred
551 Finches, with Crimson Finches being intermediate. These data add to that on diet, seasonal
552 movements and habitat use (Dostine and Franklin 2002) in demonstrating fine
553 ecological/resource partitioning among this speciose finch assemblage. The results are also
554 consistent with comparative studies of body condition across finch species in the tropical
555 savannas that have identified Gouldian Finches as being particularly responsive to changes in
556 the spatio-temporal availability of grass seed (Legge et al. 2015; Maute et al. 2015).

557

558

559 **Geolocation details**

560

561 Our study was conducted at Mornington Wildlife Sanctuary (17°30'S, 126°07'E), a 3,210
562 km² conservation reserve in the central Kimberley region of northern Western Australia

563

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565

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573

574 **References**

575

576 Anderson, M. J., Gorley, R. N., and Clarke, K. R. (2008). '*PERMANOVA+ for PRIMER:*

577 *Guide to Software and Statistical Methods.*' (PRIMER-E: Plymouth, UK.)

578 Areta, J. I., Bodrati, A., and Cockle, K. (2009). Specialization on *Guadua* bamboo seeds by
579 three bird species in the Atlantic forest of Argentina. *Biotropica* **41**, 66-73.

580 Baldwin, M. W., Winkler, H., Organ, C. L., and Helm, B. (2010). Wing pointedness

581 associated with migratory distance in common-garden and comparative studies of

582 stonechats (*Saxicola torquata*). *Journal of Evolutionary Biology* **23**, 1050-1063.

- 583 Blendinger, P. G., and Ojeda, R. A. (2001). Seed supply as a limiting factor for granivorous
584 bird assemblages in the Monte Desert, Argentina. *Austral Ecology* **26**, 413-422.
- 585 Bortolotti, G. R., Dawson, R. D., and Murza, G. L., (2002). Stress during feather
586 development predicts fitness potential. *Journal of Animal Ecology* **71**, 333-342.
- 587 Brandt, M. J., and Cresswell, W. (2008). Breeding behaviour, home range and habitat
588 selection in Rock Firefinches *Lagonosticta sanguinodorsalis* in the wet and dry
589 season in central Nigeria. *Ibis* **150**, 495-507.
- 590 Brazill-Boast, J., Pryke, S. R., and Griffith, S. C. (2010). Nest-site utilisation and niche
591 overlap in two sympatric, cavity-nesting finches. *Emu* **110**, 170-177.
- 592 Brown, J. S., Kotler, B. P., and Mitchell, W. A. (1994). Foraging theory, patch use, and the
593 structure of a Negev Desert granivore community. *Ecology* **75**, 2286-2300.
- 594 Dawson, A., and Newton, I. (2004). Use and validation of a molt score index corrected for
595 primary-feather mass. *Auk* **121**, 372-379.
- 596 de la Hera, I., Diaz, J. A., Perez-Tris, J., and Telleria, J. L. (2009). A comparative study of
597 migratory behaviour and body mass as determinants of moult duration in passerines.
598 *Journal of Avian Biology* **40**, 461-465.
- 599 de la Hera, I., Perez-Tris, J., and Telleria, J. L. (2010). Migratory behavior and differential
600 resource allocation between wing and tail feathers in a passerine bird. *Auk* **127**, 647-
601 652.
- 602 Dostine, P. L., and Franklin, D. C. (2002). A comparison of the diet of three finch species in
603 the Yinberrie Hills area, Northern Territory. *Emu* **102**, 159-164.
- 604 Dostine, P. L., Johnson, G. C., Franklin, D. C., Zhang, Y., and Hempel, C. (2001). Seasonal
605 use of savanna landscapes by the Gouldian finch, *Erythrura gouldiae*, in the Yinberrie
606 Hills area, Northern Territory. *Wildlife Research* **28**, 445-458.
- 607 Eggers, S., and Low, M. (2014). Differential demographic responses of sympatric Parids to
608 vegetation management in boreal forest. *Forest Ecology and Management* **319**, 169-
609 175.
- 610 Evans, S. M., Collins, J. A., Evans, R., and Miller, S. (1985). Patterns of drinking behaviour
611 of some Australian estrildine finches. *Ibis* **127**, 348-354.
- 612 Franklin, D. C., Dostine, P. L., and Tidemann, S. C. (1998). Post-juvenile moult strategies of
613 co-existing Gouldian, Long-tailed and Masked Finches. *Corella* **22**, 73-79.
- 614 Garb, J., Kotler, B. P., and Brown, J. S. (2000). Foraging and community consequences of
615 seed size for coexisting Negev Desert granivores *Oikos* **88**, 291-300.
- 616 Ginn, H. B., and Melville, D. S. (1983). 'Moult in birds.' (British Trust for Ornithology:

617 Tring.)

618 Hall, K. S. S., and Tullberg, B. S. (2004). Phylogenetic analyses of the diversity of moult
619 strategies in Sylviidae in relation to migration. *Evolutionary Ecology* **18**, 85-105.

620 Higgins, P. J., Peter, J. M., and Cowling, S. J. (Eds.) (2006). ‘Handbook of Australian, New
621 Zealand & Antarctic Birds. Volume 7. Boatbill to Starlings.’ (Oxford University
622 Press: South Melbourne.)

623 Jovani, R., and Blas, J., (2004). Adaptive allocation of stress-induced deformities on bird
624 feathers. *Journal of Evolutionary Biology* **17**, 294-301.

625 Jovani, R., Blas, J., Stoffel, M., Bortolotti, L., and Bortolotti, G. R. (2010). Fault bars and the
626 risk of feather damage in cranes. *Journal of Zoology* **281**, 94-98.

627 Jovani, R., and Rohwer, S. (2016). Fault bars in bird feathers: mechanisms and ecological and
628 evolutionary causes and consequences. *Biological Reviews Online* early doi:
629 10.1111/brv.12273

630 Kaboli, M., Aliabadian, M., Guillaumet, A., Roselaar, C. S., and Prodon, R. (2007).
631 Ecomorphology of the wheatears (genus *Oenanthe*). *Ibis* **149**, 792-805.

632 Kjellen, N. (1994). Moulting in relation to migration in birds - a review. *Ornis Svecica* **4**, 1-24.

633 Legge, S., Garnett, S., Maute, K., Heathcote, J., Murphy, S., Woinarski, J. C. Z., and
634 Astheimer, L. (2015). A landscape-scale, applied fire management experiment to
635 promote recovery of a population of the threatened Gouldian finch, *Erythrura gouldiae*,
636 in Australia’s tropical savannas. *Plos One* DOI:10.1371/journal.pone.0137997.

637 Lewis, M. (2007). Foraging responses of the endangered Gouldian Finch to temporal
638 differences in seed availability in northern Australian savanna grasslands. In
639 ‘Temporal Dimensions of Landscape Ecology - Wildlife Responses to Variable
640 Resources.’ (Ed. J.A. Bissonette and I. Storch.) pp. 218-235. (Springer: New York.)

641 Ley, A., and Tynan, B. (2011). An irruption of pictorella mannikins. *Australian Field*
642 *Ornithology* **28**, 114-119.

643 Lockwood, R., Swaddle, J. P., and Rayner, J. M. V. (1998). Avian wingtip shape
644 reconsidered: wingtip shape indices and morphological adaptations to migration.
645 *Journal of Avian Biology* **29**, 273-292.

646 Lowe, K. W. (1989). ‘The Australian Bird Bander's Manual.’ (Australian National Parks and
647 Wildlife Service: Canberra.)

648 Maute, K., French, K., Legge, S., and Astheimer, L. (2013). Seasonal stress physiology and
649 body condition differ among co-occurring tropical finch species. *Journal of Comparative*
650 *Physiology B* DOI 10.1007/s00360-013-0775-y

651 McDonald, N. S., and McAlpine, J. (1991). Floods and droughts: the northern climate. In
652 'Monsoonal Australia. Landscape, ecology and man in the northern lowlands.' (Ed. C.
653 D. Haynes, M. G. Ridpath, and M. A. J. Williams.) pp. 19-29. (AA Balkema:
654 Rotterdam.)

655 Mila, B., Wayne, R. K., and Smith, T. B. (2008). Ecomorphology of migratory and sedentary
656 populations of the Yellow-rumped Warbler (*Dendroica coronata*). *Condor* **110**, 335-
657 344.

658 Milenkaya, O., Legge, S., and Walters, J. R. (2011). Breeding biology and life history traits
659 of an Australasian tropical granivore, the Crimson Finch (*Neochmia phaeton*). *Emu*
660 **111**, 312-320.

661 Møller, A. P., Erritzøe, J., and Nielson, J. T., (2009). Frequency of fault bars in feathers of
662 birds and susceptibility to predation. *Biological Journal of the Linnean Society* **97**,
663 334-345.

664 Munro, U., Funnell, J. R., and Thomson, A. S. (2006). Moults in captive partially migratory
665 and sedentary Australian silvereyes (*Zosterops lateralis*) (Zosteropidae). *Journal of*
666 *Ornithology* **147**, 287-297.

667 Navarro, J., and González-Solís, J., (2007). Experimental increase of flying costs in a pelagic
668 seabird: effects on foraging strategies, nutritional state and chick condition. *Oecologia*
669 **151**, 150-160.

670 Palmer, C. (2005). Review of Radio Tracking Data from the Gouldian finch *Erythrura*
671 *gouldiae* Project - Yinberrie Hills Study Site December 1999 to August 2000.
672 Biodiversity Conservation Unit, Department of Infrastructure Planning and
673 Environment, Darwin, NT.

674 Pennycuik, C. J. (1975). Mechanics of flight. In 'Avian Biology, Vol. 5.' (Ed. D. S. Famer,
675 and J. R. King.) pp. 1-75. (Academic Press: New York.)

676 Podlasczuk, P., Kaminski, M., Włodarczyk, R., Kaczmarek, K., Janiszewski, T., and Minias,
677 P. (2016). Plumage quality mediates a life-history trade-off in a migratory bird.
678 *Frontiers in Zoology* **13**, DOI: 10.1186/s12983-016-0179-4.

679 Price, M.V., and Joyner, J.W. (1997). What resources are available to desert granivores: Seed
680 rain or soil seed bank? *Ecology* **78**, 764-773.

681 Sarasola, J. H., and Jovani, R., (2006). Risk of feather damage explains fault bar occurrence
682 in a migrant hawk, the Swainson's hawk *Buteo swainsoni*. *Journal of Avian Biology*
683 **37**, 29-35.

684 Serrano, D., Jovani, R., (2005). Adaptive fault bar distribution in a long-distance migratory,
685 aerial forager passerine? *Biological Journal of the Linnean Society* **85**, 455-461.

686 Siriwardena, G. M., Calbrade, N. A., Vickery, J. A., and Sutherland, W. J. (2006). The effect
687 of the spatial distribution of winter seed food resources on their use by farmland birds.
688 *Journal of Applied Ecology* **43**, 628-639.

689 Soobramoney, S., Perrin, M. R. (2008). A comparison of giving-up densities of five species
690 of granivorous birds *Ostrich* **79**, 101-104.

691 Suppiah, R. (1992). The Australian summer monsoon: a review. *Progress in Physical*
692 *Geography* **16**, 283-318.

693 Tidemann, S. C., Boyden, J., Elvish, R., Elvish, J., and O'Gorman, B. (1992). Comparison of
694 the breeding sites and habitat of two hole-nesting estrildid finches, one endangered, in
695 northern Australia. *Journal of Tropical Ecology* **8**, 373-388.

696 Tidemann, S. C., Lawson, C., Elvish, R., Boyden, J., and Elvish, J. (1999). Breeding biology
697 of the Gouldian Finch *Erythrura gouldiae*, an endangered finch of northern Australia.
698 *Emu* **99**, 191-199.

699 Tidemann, S. C., and Woinarski, J. C. Z. (1994). Moulting characteristics and breeding seasons
700 of Gouldian *Erythrura gouldiae*, Masked *Poephila personata* and Long-tailed Finches
701 *P. acuticauda* in savannah woodland in the Northern Territory. *Emu* **94**, 46-52.

702 Todd, M. K. (2002). Nest-site and breeding-season data for the Crimson Finch *Neochmia*
703 *phaeton* in Australia. *Australian Bird Watcher* **19**, 161-171.

704 van Rooij, E. P., and Griffith, S. C. (2011). Breeding ecology of an Australian estrildid, the
705 Long-tailed Finch (*Poephila acuticauda*). *Emu* **111**, 297-303. White AE, Gaston KJ,
706 Bronstein JL (2016) Geographical barriers and dispersal propensity interact to limit
707 range expansions of Himalayan birds. *The American Naturalist* **188**, 99-112.

708 Wood, S., Scheipl, F., (2014). gamm4: Generalized additive mixed models using mgcv and
709 lme4. R package version 0.2-3, <http://CRAN.R-project.org/package=gamm4>.

710 Woinarski, J. C. Z., and Tidemann, S. (1992). Survivorship and some population parameters
711 for the endangered Gouldian Finch *Erythrura gouldiae* and two other finch species at
712 two sites in tropical northern Australia. *Emu* **92**, 33-38.

713 Woinarski, J. C. Z., Williams, R. J., Price, O., and Rankmore, B. (2005). Landscapes without
714 boundaries: wildlife and their environments in northern Australia. *Wildlife Research*

715 **32**, 377–388.

716 Zhang, S., Wang, B. (2008). Global summer monsoon rainy seasons. *International Journal of*

717 *Climatology* **28**, 1563-1578.

718

Table 1. Attributes and sample sizes of the five study species of finch, listed in order of increasing mobility. Attributes were obtained from Higgins et al. (2006) and the personal observations of the authors in addition to the species-specific sources listed below.

Species	Body mass (g)	Habitat	Movements	Key additional sources	Study n	% juvenile	n moult assessed*	n wing shape**
Crimson Finch <i>Neochmia phaeton</i>	10.0	Riparian and adjacent savanna	sedentary, mostly very local	Todd (2002); Milenkaya et al. (2011)	1320	21.3	1000	20
Double-barred Finch <i>Taeniopygia bichenovii</i>	9.5	savanna near areas of thicker shrubs/trees	sedentary / locally nomadic		1092	4.6	932	10
Long-tailed Finch <i>Poephila acuticauda</i>	14.5	savanna	mostly sedentary but with large home ranges	Tidemann et al. (1992); Brazill-Boast et al. (2010)	1853	18.3	1592	22
Gouldian Finch <i>Erythrura gouldiae</i>	14.5	savanna	seasonally nomadic up to regional scales	Tidemann et al. (1992); Dostine et al. (2001); Lewis (2007); Brazill-Boast et al. (2010)	1316	22.3	1170	11
Pictorella Mannikin <i>Heteromunia pectoralis</i>	15.0	savanna, semi-arid shrubland	highly nomadic, with some seasonal patterns	Ley and Tynan (2011)	196	41.3	170	10
Total					5777		4864	73

* for primary moult; the number of birds assessed for secondary and tail moult was somewhat less than that for primary moult.

** after vetting; see Methods

Table 2. Estimated time to complete primary moult in one wing in three finch species, based on individuals recaptured after more than 15 days.

Species	No. of days \pm s.e.	Range	n	Notes
Crimson Finch	165 \pm 16.0	82 – 218	8	based on 6 juvs and 1 adult
Gouldian Finch	153 \pm 19.4	121 – 207	4	based on 3 juvs and 1 adult
Long-tailed Finch	223 \pm 23.8	86 – 306	10	based on 1 juv and 9 adults

Table 3. The number of primary feathers on the left wing growing at one time during moult, in five finch species from northern Australia, presented as the number and percentage of individuals with growing primary feathers.

Species	Age	<u>Number of feathers</u>			Mean	n
		One	Two	Three		
Crimson Finch	adult	40.0%	52.0%	8.0%	1.68	100
	juvenile	73.7%	24.6%	1.8%	1.28	57
Double-barred Finch	adult	78.0%	19.6%	2.3%	1.25	255
	juvenile	100%	0	0%	1.00	4
Gouldian Finch	adult	78.1%	21.9%	0%	1.22	32
	juvenile	92.3%	7.7%	0%	1.08	91
Long-tailed Finch	adult	92.2%	6.5%	1.0%	1.09	397
	juvenile	90.4%	8.7%	1.0%	1.11	104
Pictorella Mannikin	adult	100%	0%	0%	1.00	6
	juveniles	85.0%	15.0%	0%	1.15	20

Table 4. The number of waves of moult in the primary feather tract on the left wing of five finch species from northern Australia, presented as the number and percentage of individuals that had two or more growing feathers on that wing.

Species	Age	<u>Number of waves</u>			Mean	n
		One	Two	Three		
Crimson Finch	adult	95.0%	5.0%	0%	1.05	60
	juvenile	66.7%	33.3%	0%	1.33	15
Double-barred Finch	adult	23.2%	75.0%	1.8%	1.79	56
	juvenile	-				
Gouldian Finch	adult	85.7%	14.3%	0%	1.14	7
	juvenile	100%	0%	0%	1.00	8
Long-tailed Finch	adult	61.3%	38.7%	0%	1.39	31
	juvenile	80.0%	20.0%	0%	1.20	10
Pictorella Mannikin	adult	-				0
	juvenile	100%	0%	0%	1.00	3

Table 5. Model summary from GAMM investigating the incidence of feather faults in five species of finch from northern Australia. The model compares against factors Crimson Finch, primaries and adult.

	Estimate	S. E.	Wald test z	Pr(> z)
Intercept	-3.316	0.083	-40.12	< 0.001
Double-barred Finch	-0.580	0.104	-5.58	< 0.001
Gouldian Finch	-0.693	0.096	-7.19	< 0.001
Long-tailed Finch	-0.343	0.091	-3.79	< 0.001
Pictorella Mannikin	-1.229	0.209	-5.87	< 0.001
Secondaries	0.292	0.050	5.89	< 0.001
Tail	2.450	0.044	55.23	< 0.001
Juvenile	-0.099	0.092	-1.07	0.284
s(Month)	0.883	0.137	6.45	< 0.001

Table 6. Summary of the results of the key analyses examining variation in wing morphology, moult patterns and feather faulting in relation to the relative mobility of five finch species in northern Australia.

Wing morphology, feather and moult attributes		Mobility of finch species (highest to lowest)								
		PM	>	GF	>	LTF	>	DBF	>	CF
Wing Morphology										
Aspect ratio:	prediction (mobility)	highest								lowest
	observed	3.6 (highest)	3.9	3.5	3.0	2.6				
Wing loading:	prediction (mobility)	highest								lowest
	observed (kg/m ²)	2.2 (highest)	2.3	2.1	1.7	1.7				
Moult patterns										
Population synchrony:	predicted	shortest								longest
	observed (rank)	1 st (shortest)	1 st	3 rd	3 rd	5 th				
Feathers moulted:	predicted	1								> 1
	observed (adult mean)	1	1.2	1.1	1.3	1.7				
Moult waves:	predicted	1								> 1
	observed (adult mean)	1	1.1	1.4	1.8	1.1				
Feather growth rate:	predicted	fastest								slowest
	observed (rank)		1 st	3 rd		1 st (slowest)				
Feather faults										
Fault incidence:	prediction	lowest								highest
	observed (rank)	lowest	4th	2nd	3rd	1 st (highest)				

Figure legends

Figure 1. Wing morphology (aerodynamic attributes) of five north Australian finch species. Crosses intersect at species centroids and depict the 95% confidence interval for the mean. Dashed lines are convex polygons around all values. Sample sizes are: Crimson Finch – 20; Double-barred Finch – 10; Long-tailed Finch – 22; Pictorella Mannikin – 10; Gouldian Finch – 11.

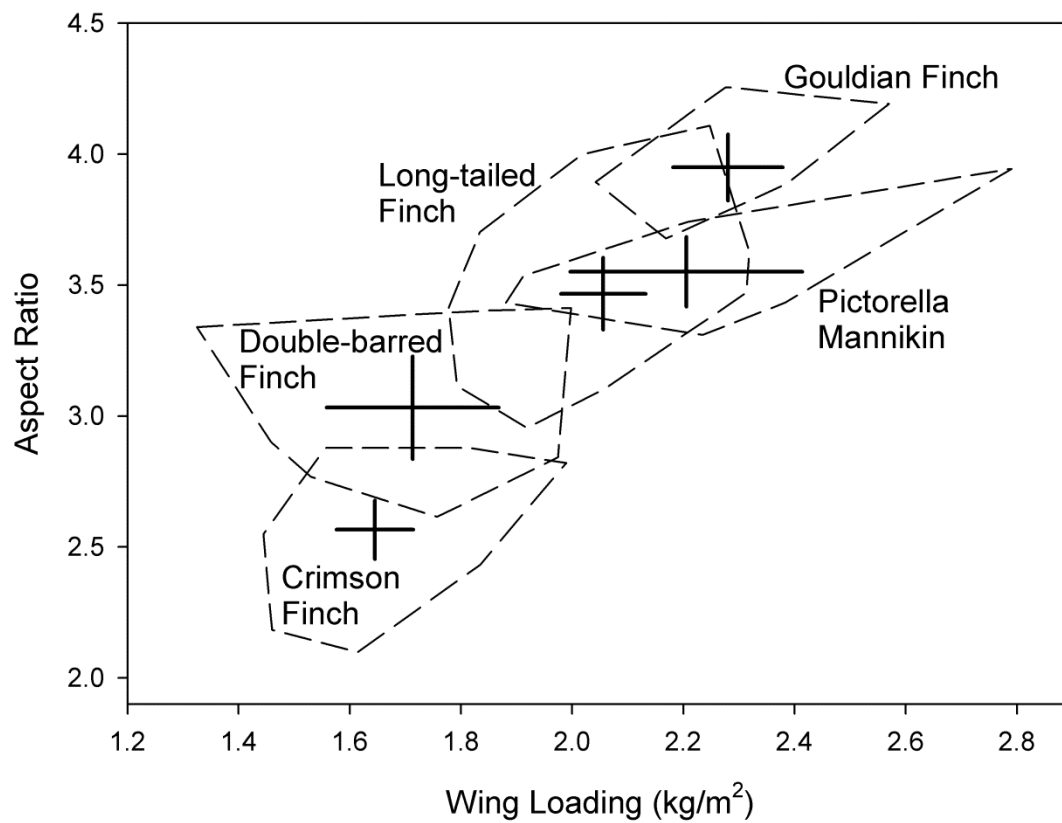


Figure 2. Timing of moult of flight feathers in adult birds for four species of finch from northern Australia, as indicated by the occurrence of growing feathers (moult scores 1-4), against the background of the percentage of the population that were recognisable as juveniles. All species are represented by at least 12 birds in each month but mostly by many more.

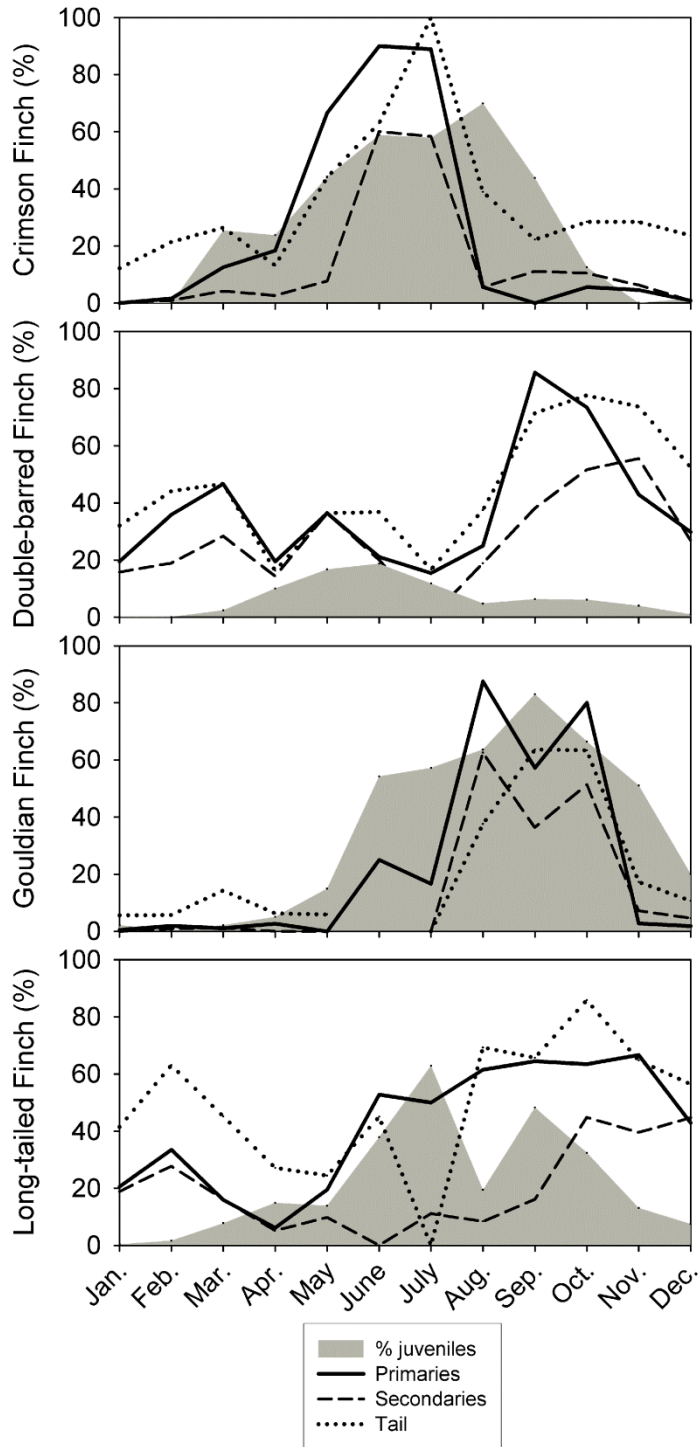


Figure 3. The incidence of feather faults among species. Partial coefficients from the GAMM model are shown with standard errors. Crimson Finches have the greatest incidence of faulting; Pictorella Mannikins have the least.

