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

Abstract

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

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

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Introduction

To minimise the energetic demands of long-distance flight, the wings of migratory birds have a higher aspect ratio (i.e. are longer and narrower) and are more pointed and convex than less mobile relatives (Lockwood et al. 1998; Mila et al. 2008; Baldwin et al. 2010). High aspect ratios reduce the mechanical power needed for flight (Norberg 2012). The wing loading (weight per unit wing area) of migrants is variable, and depends on how fast they need to fly: combined with a high aspect ratio, low wing loading reduces the power needed to fly, but also reduces the flight speed. Fast-flying migrants may therefore combine a high aspect ratio with a relatively high wing loading (Norberg 2012). Migratory birds also moult more rapidly (Kjellen 1994; de la Hera et al. 2009) and avoid moulting during migration (Podlaszczuk et al. 2016), in order to avoid compromising the flight surfaces and reducing flight performance (Navarro and Gonzalez-Solis 2007).

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

Several studies suggest that locally-migratory or nomadic species are subject to similar selective pressures on wing morphology and moult patterns as long distance migrants, albeit to a lesser degree. For example wheatears (*Oenanthe* spp.) occupying arid regions have more pointed wings than those of less-arid regions, plausibly because birds in arid regions have to track sparse food resources at greater spatial scales; however, they had less-pointed wings than congeners that migrate long distances (Kaboli et al. 2007). Similarly, within the warbler family, moult strategy varied with migration distance (Hall and Tullberg 2004). In a broader comparative review, de la Hera et al. (2009) found that the time taken to complete moult in short-distance migrants was intermediate between that of sedentary species and long-distance migrants. Finally, Silvereyes (*Zosterops lateralis*) from a partially-migratory population in Australia commence moult earlier and on a more fixed schedule than members of a sedentary population of the same species (Munro et al. 2006). These trends have mostly been identified from high-latitude regions. Trends may differ in tropical areas as they provide a longer season that is suitable for moult and breeding. Furthermore, tropical nomads may have less rigid annual schedules than higher latitude species, and their need to move is less predictable; this may render some overlap between moult, breeding and major movements unavoidable in tropical areas.

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

Niche separation along a spectrum of levels of mobility may partly explain the co-existence of 11 sympatric species of grass-finch in the tropical savannas of the Kimberley region of north-western Australia. They range in mass from 7.5 – 15 g, but display little morphological variation in bill types (Higgins et al. 2006). Their feeding behaviour is similar; they eat grass-seed, usually from the ground but also from standing grass stalks (in the wet season). There is some separation of species by habitat, but mixed-species flocks are a common seasonal occurrence. Despite these ecological similarities, there is marked interspecific variation amongst finches in their sensitivity to contemporary land use changes. Variation in mobility may also relate to this, because changed fire regimes and grazing by introduced herbivores have modified the spatio-temporal availability of grass seed (Maute et al. 2013; Legge et al. 2015).

In this study, we compare and contrast the wing morphology (wing loading, aspect ratio), flight feather fault patterns and moult strategies of five sympatric finch species (Estrildidae) from the tropical Kimberley region of northern Australia (Table 1). These species all feed on grass seed and live in broadly similar habitats. However, they vary in mobility, from occupying small home ranges throughout the year to being nomadic at scales of tens or even hundreds of kilometres (reviewed below). If the physical implications of resource-tracking at contrasting spatial scales provide a unifying set of selective forces in these finches, then we anticipate a positive association between mobility, wing loading and aspect ratios (to allow fast and energy-efficient flight; Norberg 2012); a negative association between mobility and the incidence of feather faults; and that more mobile species will reduce gaps in the flight surface of their wings by rapidly moulting one feather at a time (Pennycuick 1975).

Methods

Study area and species

Our study was conducted at Mornington Wildlife Sanctuary (17°30’S, 126°07’E), a 3,210 km^2 conservation reserve in the central Kimberley region of northern Western Australia, managed by the Australian Wildlife Conservancy (http://www.australianwildlife.org/). The climate is monsoonal tropical, with a mean annual rainfall of c. 750 mm. Temperatures are high throughout the year. The predominant vegetation types are semi-arid lowland savanna (grassland with scattered trees including *Eucalyptus* spp., *Corymbia* spp., *Bauhinia cunninghamii* and *Adansonia gregorii*, and sandstone hills and escarpments with spinifex hummock grasses (*Triodia* spp.). The Sanctuary has a number of permanent and semi-permanent watercourses including the Fitzroy, Hann and Adcock Rivers which support narrow bands of riparian forest; the sandstone areas also feature many permanent waterholes.

Australian finches have nine primaries and eight secondaries (including three tertials) per wing, and 12 rectrices (tail feathers) (Higgins et al. 2006). Primary moult is descendant (from the inside out). Adults of the study species undertake a complete annual pre-basic moult. There is no pre-alternate moult (no moult into a distinct breeding plumage). Juveniles of all our study species moult directly into adult plumage. With the exception of the Gouldian Finch *Erythrura gouldiae*, juvenile plumage of our study species differs from adult plumage only by degrees and often subtly, and no species can be readily aged by its flight feathers. Full adult body plumage is usually gained within two to nine months of hatching, the period being longest in the Gouldian Finch and Pictorella Mannikin *Heteromunia pectoralis* (Higgins et al. 2006). The post-juvenile moult is complete or believed to be complete in three species, but not in Gouldian or Crimson Finches *Neochmia phaeton* (Franklin et al. 1998; Milenkaya et al. 2011).

TABLE 1 near here

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

Field data

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

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

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

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

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

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

Data analysis

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

$$AR = ((2 * WL)^2) / (2 * WA)$$

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

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

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

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

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

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

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

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

Results

Wing morphology

Rank ordering of finch species according to wing loading and aspect ratio were identical, Gouldian Finches having the highest values and Crimson Finches the lowest of both measures (Fig. 1). Considered both as individual attributes and as points in multi-variate space, the five finch species differed with respect to both measures (wing loading, $F_{4,68}$ = 31.5, $P < 0.0001$; aspect ratio, $F_{4,68}$ = 65.4, $P < 0.0001$; in multivariate space, pseudo-$F_{4,68}$ = 53.5, $P = 0.0001$). Post-hoc comparisons of position in multivariate space demonstrated that all species-pairs were separable ($P < 0.01$) except Pictorella Mannikin and Long-tailed Finch ($P = 0.20$).

FIGURE 1 near here

Moulting patterns

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

FIGURE 2 near here

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

Moult of secondaries (and to a lesser extent tail feathers) in adult Crimson, Double-barred and Long-tailed Finches loosely followed primary moult with a delay of up to several months (Fig. 2). In the Gouldian Finch, however, moult of secondaries and tail feathers was strongly coincident with that of primary moult, accentuating the population-level synchronicity of moult.

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

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

The nature of primary moult

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

TABLE 2 near here

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

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

TABLE 3 near here

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

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

TABLE 4 near here

Feather faults

Faults were quantified in 51,154 feathers sampled from 2,340 finches. A high proportion of feathers sampled were free of faults (89.6%) but 1.4% had incomplete faults, 0.2% had complete faults, 8.9% had incomplete breaks and 0.7% had complete breaks. For those feathers with faults, the majority had only one (68.7%) or two faults (18.9%). 1.5% of feathers with damage had more than six faults, with the maximum number being twenty per feather (n = 1). All feathers with more than six faults were tail feathers. Faults were not distributed evenly among feather types. Only 4% of primaries and 5% of secondaries had some form of faulting, compared to 27% of tail feathers.

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

TABLE 5 near here

FIGURE 3 near here

Discussion

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

Alternative explanations for the variation in wing morphology, feather faulting and moulting can be discounted.. The five species vary 1.5 fold in body mass, and body mass is related to some of the attributes we measured, but usually in ways opposite to the observed patterns. For example, feather replacement in larger birds takes longer, so they generally take longer to moult; to partially compensate they grow their feathers faster and may moult more than one feather at a time (Rohwer et al. 2009); however, in our study, the larger finches moulted over a shorter period, did not clearly grow feathers faster, and were less likely to moult more than a single feather at a time. Wing loading generally increases allometrically with bird mass, but aspect ratio is independent of body mass in geometrically similar birds (Norberg 2012), so the variation observed cannot be explained by differences in body mass.

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

The incidence of feather faults was broadly consistent with our expectations, with Pictorella Mannikins having fewest faults, and Crimson Finches having most. However, the incidence of feather faults in Gouldian Finches was only slightly less than for Double-barred Finches, and Long-tailed Finches had more faults than Double-barred Finches. Although species and feather types may fundamentally differ in their propensity to produce fault bars, the incidence of fault bars can also be modified by stressors experienced by individual birds during their moult (Jovani et al 2016). The surprisingly high fault rates in both the Gouldian and Long-tailed Finches could arise if those species experience stress during their moulting period as a result of contemporary land management practices, as has been suggested elsewhere (Dostine et al. 2001; Dostine and Franklin 2002; Legge et al. 2015; Maute et al. 2015).

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

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

Conclusion

Whilst wing morphologies and feather fault patterns corresponded with levels of mobility in our five study species, moult strategies were less strongly aligned and presumably reflect additional life history complexities and environmental stressors. The seasonality and rate of moult varied considerably among species with an apparent gradation between relatively rapid, strongly-seasonal moult in Gouldian Finches (and probably Pictorella Mannikins), through to the slower and/or less seasonal moult in Long-tailed and especially Double-barred Finches, with Crimson Finches being intermediate. These data add to that on diet, seasonal movements and habitat use (Dostine and Franklin 2002) in demonstrating fine ecological/resource partitioning among this speciose finch assemblage. The results are also consistent with comparative studies of body condition across finch species in the tropical savannas that have identified Gouldian Finches as being particularly responsive to changes in the spatio-temporal availability of grass seed (Legge et al. 2015; Maute et al. 2015).

Geolocation details

Our study was conducted at Mornington Wildlife Sanctuary (17°30'S, 126°07'E), a 3,210 km^2 conservation reserve in the central Kimberley region of northern Western Australia

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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 *Neochmia phaeton*	10.0	Riparian and adjacent savanna	sedentary, mostly very local	Todd (2002); Milenkaya et al. (2011)	1320	21.3	1000	20
Double-barred Finch *Taeniopygia bichenovii*	9.5	savanna near areas of thicker shrubs/trees	sedentary / locally nomadic		1092	4.6	932	10
Long-tailed Finch *Poephila acuticauda*	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 *Erythrura gouldiae*	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 *Heteromunia pectoralis*	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 ± s.e.	Range	n	Notes
Crimson Finch	165 ± 16.0	82 – 218	8	based on 6 juvs and 1 adult
Gouldian Finch	153 ± 19.4	121 – 207	4	based on 3 juvs and 1 adult
Long-tailed Finch	223 ± 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.

		Number of feathers				
Species	Age	One	Two	Three	Mean	n
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.

		Number of waves				
Species	Age	One	Two	Three	Mean	n
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)	1st (shortest)	1st	3rd	3rd	5th
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
Moult rate:	predicted	fastest				slowest
	observed (rank)		3rd	1st		3rd (slowest)
Feather faults						
Fault incidence:	prediction	lowest				highest
	observed (rank)	lowest	4th	2nd	3rd	1st (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. Only the Long-tailed Finch and the Pictorella Mannikin are not separable in post-hoc comparisons. 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. Species are ordered top to bottom according to mobility (with top being least mobile, bottom being most mobile). 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. Species are ordered along the x-axis according to mobility (with left being least mobile, right being most mobile).