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POST-JUVENILE MOULT STRATEGIES OF CO-EXISTING GOULDIAN, LONG-TAILED AND MASKED FINCHES

DONALD C. FRANKLIN,[1] P. L. DOSTINE[1] and SONIA C. TIDEMANN[1,2]

[1]Parks and Wildlife Commission of the Northern Territory, P.O. Box 496, Palmerston, Northern Territory 0831 *and*
Cooperative Research Centre for the Sustainable Development of Tropical Savannas, Northern Territory University, Darwin, Northern Territory 0909
[2]*Current address:* Batchelor College, Batchelor, Northern Territory 0845

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The post-juvenile moult strategies of three co-existing woodland finch species in monsoonal northern Australia were compared. Juvenile Gouldian Finches tended to moult at the same time of year as each other regardless of age, whereas in juvenile Long-tailed and Masked Finches the commencement of moult was progressive through the year and may be related more directly to the age of the individual. Gouldian Finches retained obvious juvenile characters for longer than the other species. Juvenile Gouldian Finches undertook only a partial post-juvenile primary moult in their first year whereas in the Long-tailed and Masked Finch, the primary moult was complete. Primary moult of juvenile Masked Finches was more rapid than that of either Gouldian or Long-tailed Finches. In all three species, the post-juvenile primary moult occurred at the same time as that of adults. Juvenile Long-tailed and Masked Finches undertook this moult at a similar rate to adults. In contrast, the post-juvenile primary moult of the Gouldian Finch was much slower than that of adults, and the partial primary moult is probably required in order to finish the moult prior to Wet season dispersal. Juvenile Gouldian Finches moult at a time of the year when food availability is low. This is a seemingly anomalous and potentially stressful situation about which they may have little evolutionary choice given that Gouldian Finches are highly mobile exploiters of ephemeral food sources in the Wet season.

INTRODUCTION

Under normal circumstances, most birds replace all their feathers once per year during a discrete moulting period. Additional protein is required for this process and in passerines basal metabolic rates are elevated during moult, sometimes by up to 100 per cent above normal (Jenni and Winkler 1994), even though moult is staggered over several to many months (Ginn and Melville 1983). In addition, moult of flight feathers has the potential to compromise flight capabilities, so that either or both the timing and sequence of flight feather moult may be important to survival.

For juveniles, which may be undergoing physiological changes related to maturing and may be less proficient than adults at finding food, moult is potentially an even more stressful process. In multi-brooded Australian honeyeaters (Meliphagidae), late-hatched young may defer part or all of the moult until the following year whereas early-hatched young moult with the adults at the end of the breeding season (e.g. Paton 1982; Franklin *et al.*, in press). In Eurasian Tree Sparrows *Passer montanus* in central Poland, both adults and young of the year undergo a complete moult in late summer and early autumn, and then become sexually active, pair up, occupy nest holes and build nests. However, late-hatched young commence and complete moult later than early-hatched young and therefore have less chance of occupying a good-quality nest hole, suggesting that there may be a very direct impact of post-juvenile moult on subsequent reproductive success (Myrcha and Pinowski 1970). In captive Gouldian Finches *Erythrura gouldiae*, mortality is strongly concentrated amongst juveniles undertaking their first moult (Koenig 1953; Murray 1953; Evans and Fidler 1986).

Tidemann and Woinarski (1994) compared primary moult strategies of adult Gouldian Finch and adults of the co-existing Long-tailed Finch *Poephila acuticauda* and Masked Finch *P. personata.* They found that Gouldian Finches had a shorter breeding season and a rapid moult which did not commence until after the completion of breeding. In contrast, at least the Long-tailed Finch had a longer breeding season and moulted more slowly, overlapping the two activities extensively. The more mobile Gouldian Finch completed moult earlier in the year, before the onset of the main rains of the Wet season when they disperse from their breeding grounds (Tidemann 1993).

In the wild, the Gouldian Finch has suffered a considerable decline in abundance and is listed as endangered (Garnett 1992; ANCA 1994). Previous papers have compared breeding sites (Tidemann *et al.* 1992), population dynamics (Woinarski and Tidemann 1992) and adult moult strategies (Tidemann and Woinarski 1994) of the Gouldian Finch and co-existing finch species. Our aim in this paper is to compare the post-juvenile moult strategies of Gouldian, Long-tailed and Masked Finches and to relate these to the adult moult strategies of the species as described by Tidemann and Woinarski (1994).

METHODS

Data collection

Most data were collected in the Yinberrie Hills (14°08'S, 132°05'E), 45 km NNW of Katherine, Northern Territory, and on Newry Station

(16°04'S, 129°05'E), 150 km WSW of Timber Creek, Northern Territory. These finch study sites have been described previously (Woinarski and Tidemann 1992), and the vegetation of core Gouldian Finch habitat in the Yinberrie Hills was described in detail by Bowman *et al.* (1991). A few banding and moult records were also collected at other sites in the Northern Territory and the Kimberley region of Western Australia, most particularly in the vicinity of Timber Creek (15°40'S, 130°28'E).

Finches were caught in mist nets or clap traps and banded in every year and on numerous occasions from 1986 to 1997. Most banding was done during the dry season months of May to October, usually when birds came to drink at waterholes. Limited Wet season work was conducted by capturing birds at feed sites, mainly during 1995–96. During the years 1988 to 1991 inclusive, nestling Gouldian Finches (n = 344) and Long-tailed Finches (n = 45) were banded, mostly at Newry Station but also in the Yinberrie Hills.

Captured birds were aged as juveniles or adults. Juvenile Gouldian Finches are predominantly grey below and on the crown, and olive on the back and wings, in marked contrast to the colourful adults; birds were classed as juvenile if any juvenile feathers persisted. The plumage of juvenile and adult Long-tailed and Masked Finches differ mainly in the intensity of coloration and the differences are neither great nor categoric. Estrildine finches are amongst the few Australian passerines in which there is no real difference in the plumage texture of juveniles and adults (W. Boles, pers. comm.). However, juveniles begin life with bills that are dark grey, and this gradually changes to pure and intense yellow (Masked Finch) or pure yellow, orange, pink or red (Long-tailed Finch); these species were therefore classed as juvenile if there was any trace of grey in the bill. During 1989, 1991 and from 1995 onwards, juveniles were scored for primary moult in one wing following the system of Snow (1967) and Rogers (1989) in which each feather is scored from 0 (old) to 5 (new).

Data analysis

'First-year' birds include all juveniles (except a very few that were demonstrably in their second year), plus those adults recaptured in the same year in which they were previously assessed as juvenile. 'Synchronous moult', 'asynchronous moult' and related phrases are used in this paper only in a population context to describe tendencies for individuals to moult or not to moult at the same time as each other. Primary moult scores are the sum of the scores for each primary. Primary moult rates were estimated using individuals captured more than once and at an interval of more than 15 days during the same moult cycle. The large variances associated with our small-sample estimates of these rates may reflect that primary moult does not necessarily occur at a constant rate, as well as individual variation in these rates. Confidence intervals for these rates were calculated using the Student's t correction for sample size. Primary moult rates of the species were compared using Kruskal-Wallis non-parametric analysis of variance (Zar 1984). To examine seasonal shifts in the distribution of primary moult scores, we selected sampling periods when more than 20 first-year birds were scored at a study area within a maximum of seven consecutive days. Dates attached to each sample are the median collection date, and results are presented only for the study area with the best spread of samples through the year for the finch species concerned. Moult terminology follows Ginn and Melville (1983).

RESULTS

General rate of development

Gouldian Finches banded as nestlings retained clear evidence of juvenility for up to 87 days and in one instance much longer (Table 1). No Gouldian Finches banded as nestlings were recaptured as adults in the year of banding. A much larger sample of birds banded and recaptured as juveniles suggests an even longer period of retention of juvenile plumage, often in excess of 100 days. In addition, there are two confirmed and two further plausible cases of Gouldian Finches banded as juveniles or nestlings and recaptured the following year whilst still retaining some juvenile plumage, in all cases more than 12 months later.

No Long-tailed Finches in a small sample that were banded as nestlings were recorded to retain evidence of juvenility for longer than 62 days, and two birds banded as nestlings and recaptured after fledging were in adult plumage at 96 and 126 day intervals (Table 1). A large sample of birds banded and recaptured as juveniles retained evidence of juvenility for no more than 63 days.

No Masked Finches were banded as nestlings. Of 130 Masked Finches banded and recaptured as juveniles, none was recaptured at an interval of greater than 47 days (Table 1).

Primary moult

All three species have nine primaries and moult their primaries in descendent sequence (i.e. from the inner primaries outwards). However, first-year Gouldian Finches were, with one exception, not recorded with primary moult scores of less than 15, in marked contrast to adult Gouldian Finches and juvenile Long-tailed and Masked Finches (Fig. 1). First-year Long-tailed and Masked Finches, in contrast, were rarely recorded with primary moult scores higher than 30.

The rarity of first-year Gouldian Finches with low primary moult scores initially perplexed us greatly, and we explored a number of explanations. Only one explanation is likely — juvenile Gouldian Finches rarely moult all their primaries. It was suggested by the observation that some birds had cohorts of primaries separable by the amount of fading, consistent with 'partial primary moult' as described by Rogers (1990). We have

TABLE 1

Summary of same-year recaptures of birds banded as nestlings or juveniles. Recapture intervals are in days. Shorter recapture invervals illustrate the minimum time required to progress from nestling to adult stages (available for Long-tailed Finch only). Longer recapture intervals illustrate the maximum time that an individual may retain juvenile plumage. n.r. = not relevant.

Species	Age at banding	Age at recapture	Number	Shorter recapture intervals	Longer recapture intervals
Gouldian Finch	nestling	juvenile	24	n.r.	131, 87, 81, 81, 77, 64, 62, 60, 49, 45, 45, 41
	nestling	adult (same year)	0		
	juvenile	juvenile	251	n.r.	164, 115, 107, 107, 107, 106, 103, 103, 97
Long-tailed Finch	nestling	juvenile	7	n.r.	62, 56, 42, 38, 25, 19, 13
	nestling	adult (same year)	2	96, 126	n.r.
	juvenile	juvenile	322	n.r.	63, 63, 63, 60, 60, 57, 56, 53, 52, 52, 51
Masked Finch	juvenile	juvenile	130	n.r.	47, 40, 39, 36, 36, 36, 36, 35, 34, 33, 32, 30

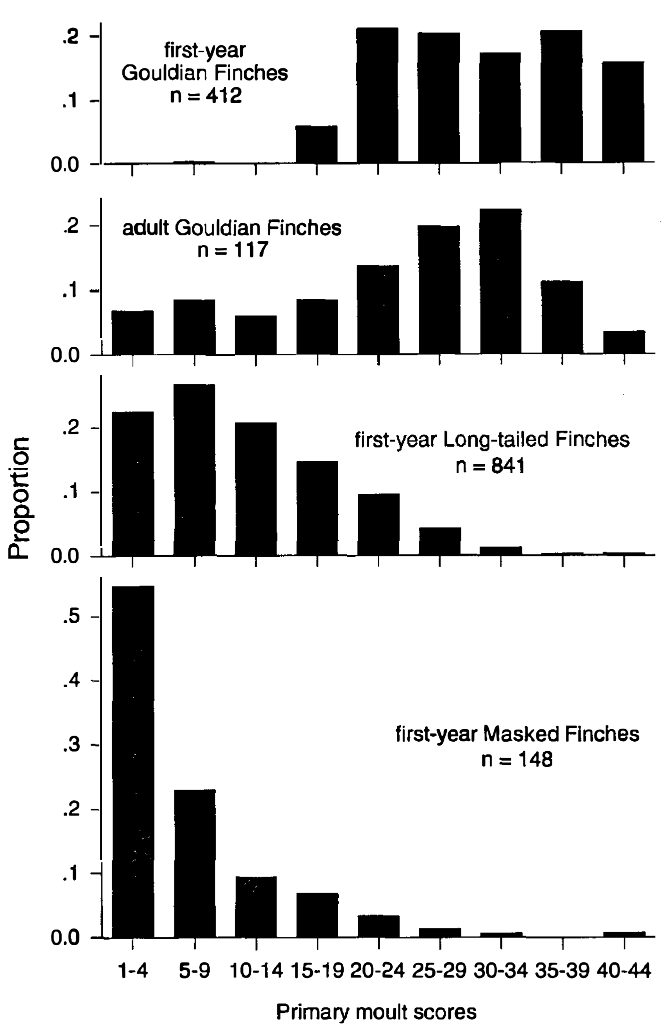

Figure 1. *Distribution of primary moult scores for all first-year and adult Gouldian Finches and first-year Long-tailed and Masked Finches that were in primary moult. For adult Gouldian Finches, data are for 1995–1997 only.*

nine written records of birds with multiple cohorts of fully-grown primaries, comprising eight juveniles and one adult. Other cases were noted but not recorded. Of the nine, one bird commenced primary moult at P3, three at P4, four at P5 and one at P6. We have also noted cases where the difference between the age of inner and outer primaries was not obvious (juvenile and adult primaries are the same colour) but the inner primary coverts were distinctly pale and juvenile whilst the outer coverts were darker (= adult). However, and in retrospect surprisingly, no distinct primary feather cohorts were evident in the majority of cases. One juvenile appeared to have undertaken or at least commenced a 'normal' full primary moult (score 531 000 000). For consistency with those where the phenomenon is assumed to exist but was not noted or noticeable, we have scored each inner, unmoulted primary as five in this and subsequent analyses.

There were very few individuals from which to calculate the rate of primary moult for first-year Gouldian and Masked Finches, and there was great variability between individuals within each species (Table 2). Nevertheless, their rates of primary moult appear to differ (Kruskal-Wallis Chi-square approximation = 5.4, d.f. = 2, $P = 0.07$), with similar moult rates in the Gouldian and Long-tailed Finch and a more rapid moult rate in the Masked Finch. Based on these mean rates, juvenile Long-tailed Finches are estimated to take 176 days to complete primary moult, juvenile Masked Finches 121 days, and juvenile Gouldian Finches 112 days to moult the outer 6 primaries, but the 95 per cent confidence interval on the estimates are broad (Long-tailed Finch 152–208 d; Masked Finch 90–185 d; Gouldian Finch 73–242 d).

The few individuals banded as nestlings and both recaptured in the same year and assessed for primary moult (Table 3) suggest that Gouldian Finches may not commence primary moult until they are more than 100 days old, perhaps twice the age of commencement in Long-tailed Finches.

TABLE 2

Primary moult rates (moult units per day) of first-year birds of three species of finch.

Species	Mean (± s.d.)	*n*
Gouldian Finch	0.267 (± 0.090)	4
Long-tailed Finch	0.256 (± 0.076)	16
Masked Finch	0.372 (± 0.124)	6

TABLE 3

Primary moult of first-year finches banded as nestlings and subsequently recaptured. The age of birds at recapture is based on the assumption that nestlings were banded at the age of 18 days, a few days before fledging (Immelmann 1982). The date of commencement of primary moult has been estimated using the moult rates in Table 2, and in the case of the Gouldian Finch, by assuming that primary moult commenced at P4. * indicates multiple recaptures of the one individual.

Species	Recapture date	Estimated age (days)	Primary moult score	Estimated age (days) at commencement of primary moult
Gouldian	02 May 91	35	00	
Finch	26 June 91	45	00	
	26 June 91	45	00	
	17 Aug. 91	82	00	
	06 July 89*	95	00	
	29 Aug. 89*	149	23	119
Long-tailed	29 Aug. 89	43	00	
Finch	15 Oct. 89	80	04	64

Population characteristics

Juvenile Gouldian Finches appeared in the population in March, formed an increasing proportion of the captures until July, remaining a high proportion of the captures until November (Fig. 2). The earliest direct evidence of primary moult was in mid-July, and backward extrapolation using the moult rate in Table 2 and the assumption that moult commenced at P4 suggests that most individuals did not commence until at least early July. Although juveniles with one or two adult-coloured feathers were caught from March to November, individuals undergoing general body moult were infrequent before August and formed a major portion of the juvenile population only in October and November. By November, at least some had completed primary moult, and most had extensive adult coloration in their plumage and advanced primary moult; a small number had little or no adult plumage and still had not commenced primary moult (Fig. 3). At least some individuals with advanced or completed primary moult in October and November were still readily recognizable as juveniles. We have few capture records of any Gouldian Finches from December to April, and none of these was juvenile. There were some differences between sites (unpubl. data) but these were slight.

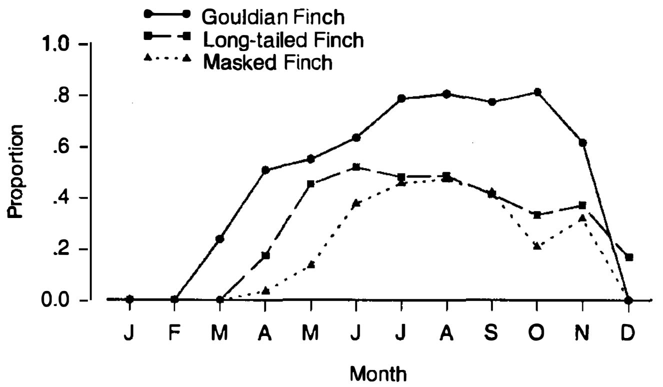

Figure 2. *The proportion of Gouldian, Long-tailed and Masked Finches caught that were juvenile (nestlings excluded), all sites and all years combined. Samples sizes for the species in order as above are: January 38, 27, 5; February 4, 12, 6; March 21, 47, 0; April 77, 81, 29; December 14, 12, 9; all other months — Gouldian Finch >250, Long-tailed Finch >300, Masked Finch >95.*

Two Long-tailed Finches were banded as nestlings in March, and juveniles began to appear in capture populations in April (Fig. 2). Proportionate capture rates increased until June and then steadily declined. Two of 12 Long-tailed Finches caught in December were juvenile. Primary moult was first observed in May, and backward extrapolation suggests that some birds commenced moult in mid-April, rarely earlier. Few juveniles were recorded in advanced primary moult (e.g. Fig. 4). Of 17 first-year birds with a primary moult score of 30 or greater, only one was definitely a juvenile on plumage or soft-part characteristics. This strongly suggests that the shortage of first-year birds with higher primary moult scores (Figs. 1, 4) was primarily due to individuals otherwise achieving full adult external characteristics before completing primary moult. They would thus mostly not be identified as first-year birds. The phenomenon may have secondarily been due to the scarcity of trapping records late in the moulting season (e.g. November, December).

Few Masked Finches and no juveniles were captured in December, January or February, and no Masked Finches were captured in March. Thereafter, the proportion of captures that were juveniles climbed slowly to a peak from June to September, declining thereafter (Fig. 2). No first-year bird was captured whilst in primary moult

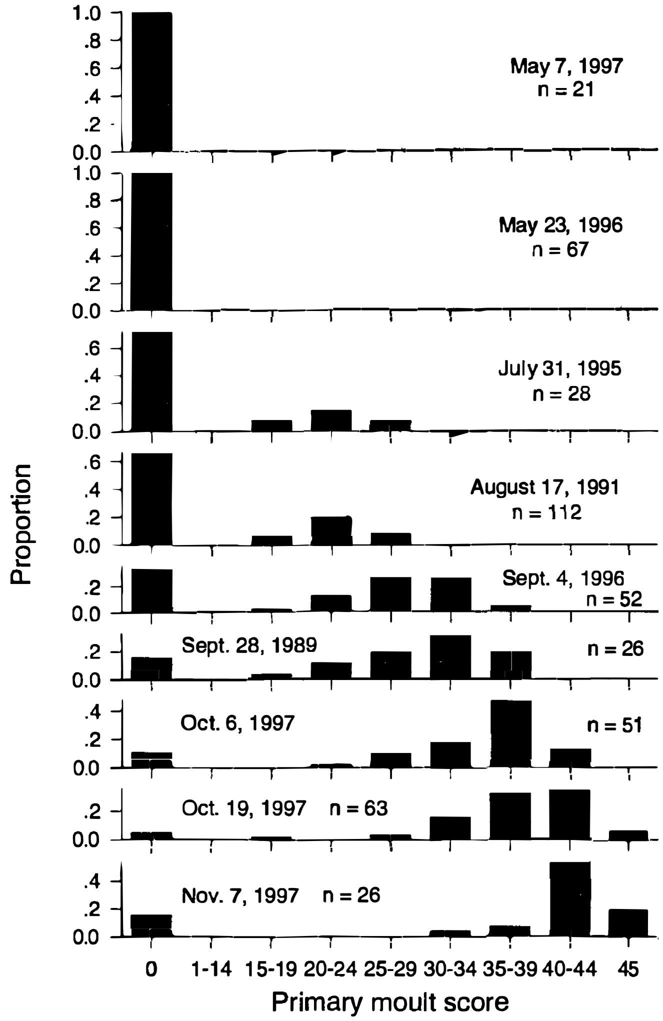

Figure 3. *Distribution of primary moult scores for first-year Gouldian Finches from the Yinberrie Hills for successive times of the year. Dates are medians for periods of up to seven days.*

before late June and few before early September (e.g. Fig. 5). Backward extrapolation suggests that the earliest commencement of primary moult was in mid-June, but that this was rare. Few juveniles were captured with primary moult scores of 20 or greater, and of the nine first-year birds that were, only two were definitely juveniles on plumage or soft-part coloration. This suggests that, as for the Long-tailed Finch, the scarcity of higher primary moult scores among first-year birds was primarily due to the rapid achievement of adult characters and our consequent failure to recognize them as first-year birds.

DISCUSSION

Moult sequences and timing

Based presumably on captive birds, Shephard (1994) noted that Gouldian Finches undertake a reasonably synchronous moult late in the year. However (and presumably also based on captive birds), Immelmann (1982), Evans and Fidler (1986) and Sammut and Marshall (1992) stated that (body) moult commences at 6–8 weeks of age, a discrepancy we cannot explain.

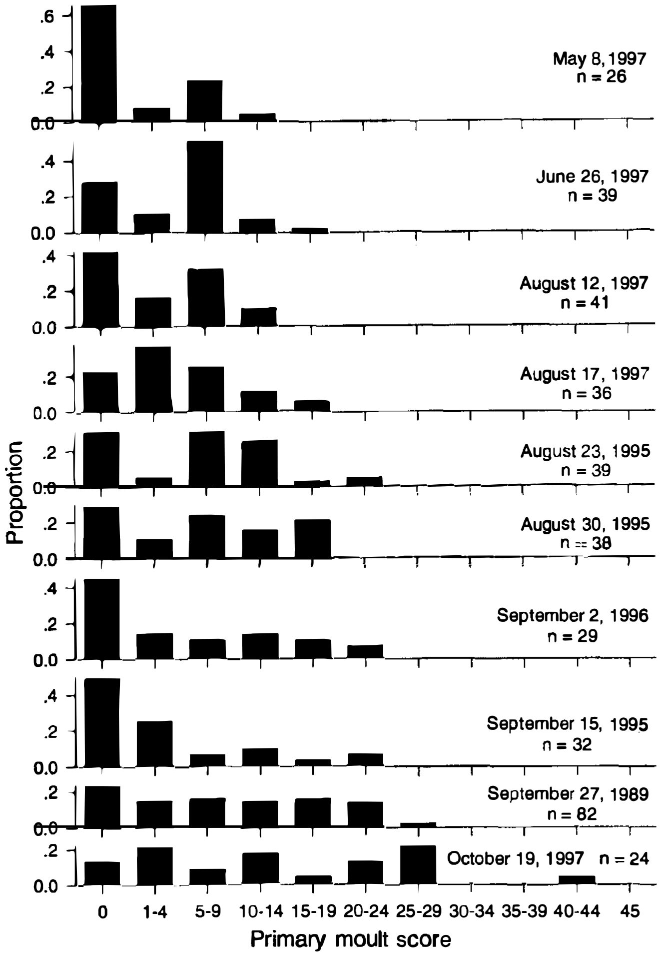

Figure 4. *Distribution of primary moult scores for first-year Long-tailed Finches from the Yinberrie Hills for successive times of the year. Dates are medians for periods of up to seven days.*

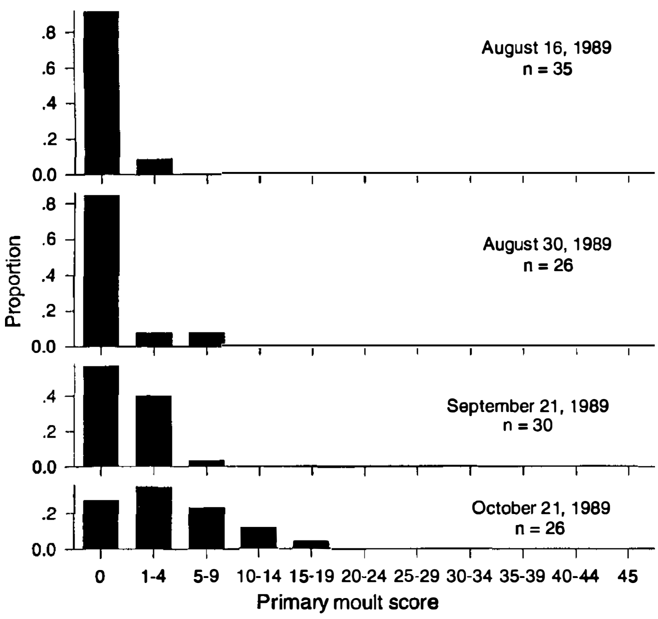

Figure 5. *Distribution of primary moult scores for first-year Masked Finches from Newry Station for successive times of the year. Dates are medians for periods of up to seven days.*

Our observation that a few Gouldian Finches failed to complete the post-juvenile moult of body feathers in their first year has also been reported in captive birds. Shephard (1994) attributed the phenomena to late hatching, but Sammut and Marshall (1992) suggested that a health 'set-back' may also cause the delay. Immelmann (1982) noted that (captive) birds in juvenile plumage may breed and suggested that moult may be delayed if conditions are suitable for young birds to breed; in the wild, the distinct seasonality of breeding by, and food supply for, Gouldian Finches (Woinarski and Tidemann 1991; Tidemann and Woinarski 1994) renders this conjunction of circumstances unlikely.

Our finding that juvenile Gouldian Finches rarely moult the inner primaries has apparently not been previously reported. That there were few recorded cases with an obvious age disjunction between the inner and outer primaries is perhaps surprising; some more individuals were detected but ignored as artefactual at the time, the significance of the phenomenon becoming evident only after the completion of data collection. That it was not recorded more often we attribute to a combination of not looking for it and that the difference between new and old feathers is much less when the old feathers are perhaps only two to five months old than when the old feathers are a year old, as in the annual moult of adults. Whether it can now be detected consistently and in birds in which the outer feathers have also had time to wear will be investigated in the near future. If it can, it should be possible to age adults that have yet to undertake their first adult moult, and in the process go a long way to resolving one of the most persistent questions in Gouldian Finch biology — whether the very low recapture rate of adults is attributable to high mortality or to some other factor such as emigration or net-shyness (Woinarski and Tidemann 1992).

That the proportional capture rates of juvenile Gouldian Finches increased during the species' breeding season (from late February to sometimes as late as August; Tidemann and Woinarski 1994) and then remained relatively constant for another four months is consistent with retention of juvenile plumage until a discrete moulting period late in the year. The progressive primary moult score distributions during the year suggest a relatively synchronous moult within the Yinberrie Hills population. In contrast, there is a decline of proportional capture rates of juvenile Long-tailed Finches after a June peak, despite the breeding season usually continuing until October (Tidemann and Woinarski 1994), and seasonal primary moult score distributions suggest an ongoing entry of young birds (and exit of older birds) from the 'population' of recognizable first-year birds. The pattern for the Masked Finch is similar to that for the Long-tailed Finch but the species' breeding season remains insufficiently defined. These observations are consistent with our admittedly scant and imprecise data on rates of moult and ageing.

Determining whether Long-tailed Finches and especially Masked Finches acquire full adult characteristics at a younger age than Gouldian Finches is complicated by several factors. Post-juvenile body moult in Gouldian

Finches is a very obvious event owing to the great contrast between juvenile and adult plumage; this stark contrast does not exist in Long-tailed and Masked Finches, and we have aged them on bill coloration instead. The latter ageing method is quite conservative, a necessity because of the range of banders involved and the demonstrably different interpretations of other ageing characteristics made by them (unpubl. data). A further complication is the likelihood that the age at which Gouldian Finches commence their post-juvenile moult varied more than in the other species. This is suggested by the relative synchronicity of moult across the Gouldian Finch population even though the species is multi-brooded in the wild (Tidemann *et al.*, in press), contrasting with the staggered seasonality of primary moult in the other species.

In Long-tailed and Masked Finches, both the timing and rate of post-juvenile primary moult appears to be similar to those of adults (this study; *cf* Tidemann and Woinarski 1994). Juvenile Gouldian Finches also undertake primary moult at the same time as adults (this study; *cf* Tidemann and Woinarski 1994), but may do so at a much slower rate (0.27 units per day; *cf* 0.74 units per day). Unfortunately, both estimates are based on very small samples and have broad confidence intervals. The incomplete primary moult of juveniles, however, may permit them to remain in synchrony with adults undertaking a complete primary moult whilst avoiding some of the costs of the adults' very rapid primary moult.

In monsoonal Zambia, Payne (1980) found that the sedentary or locally-nomadic Red-billed Firefinch *Lagonosticta senegala* commenced post-juvenile moult asynchronously over a seven month period; body moult was often finished before primary moult; primary moult was complete and took about 120 days. Asynchronous, age-dependent post-juvenile moult has been reported for the locally nomadic Zebra Finch *Taeniopygia guttata* in Victoria (Zann 1985) and amongst non-migratory European Tree Sparrows in Poland (Myrcha and Pinowski 1970). These few studies bear most resemblance to the post-juvenile moult patterns of the Long-tailed and Masked Finch.

Moult strategies

Both this study and Tidemann and Woinarski (1994) provide evidence that moult in Gouldian Finches is more tightly programmed than that of co-existing finches. Tidemann and Woinarski (1994) suggested that this may be related to the need to have completed moult (and primary moult in particular) before commencing seasonal movements. An alternative explanation for the differences we observed is phylogenetic — the Long-tailed and Masked Finches are con-generic Australian grass-finches whilst the Gouldian Finch is derived from a tropical, rainforest-edge lineage of finches, the parrot-finches (Christidis 1987). We are unaware of any studies of moult amongst parrot-finches that could clarify the issue.

In a comparison of four co-existing temperate-zone Australian grass-finches, however, Schoepfer (1988) also found that the more mobile species moulted more rapidly and completed moult before movements. Migratory fringilline and emberezine finches in Britain generally moult more rapidly than their sedentary relatives (Newton 1968). Longer-distance migrants in the Northern Hemisphere mostly commence moult after the completion of breeding and either before or after, or both before and after but not during, migration (Kjellen 1994). The problem may not be just that moult is inappropriate during migration or other periods of great mobility, but also that species undertaking regular seasonal movements of any kind must compress other activities into a shorter time period. If as a result breeding occurs at greater intensity in these species, either in the form of larger clutches or more rapid re-nesting in multi-brooded species, then the energetic demands of breeding may preclude overlap of breeding and moult. In contrast, sedentary species may breed less intensively (e.g. have smaller clutches) over a longer breeding season, the lower intensity permitting, and perhaps also the prolonged breeding season demanding, overlap of moult and breeding (Foster 1975; Franklin *et al.*, in press). Migratory or regularly mobile species clearly face additional demands and have fewer immediate and evolutionary options in their annual cycles than do sedentary species.

In captivity at least, the Gouldian Finch does have larger clutches than Long-tailed and Masked Finches (Shephard 1994), and regardless of the reason for it, the higher proportion of young in Gouldian Finch populations is likely to place greater demands on adults feeding them than in the other species. Evans *et al.* (1985) also found that juveniles form a high percentage of wild populations during the dry season. The co-incidence of the post-juvenile moult with that of adult Gouldian Finches suggests that the species' commitment to a particular life history strategy is highly evolved and inflexible.

Tidemann (1993) found Gouldian Finches to be largely absent from their breeding sites during much of the Wet season, at which time they are highly mobile in pursuit of ephemeral food sources (Dostine, Johnson and Franklin, unpubl. data). By comparison, Masked Finches appear to be sedentary, with Long-tailed Finches intermediate (unpubl. data). Such comparisons may explain why moult in the Gouldian Finch is less likely to continue after November or December than in the other species (by implication from Figs. 3, 4 and 5) and in the case of juveniles, is partly deferred until the following year. However, the result is that juvenile Gouldian Finches moult at a time of the year when food supplies are low (Woinarski and Tidemann 1991), a potentially stressful situation.

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