MORPHOLOGY, MOULT AND SURVIVAL IN THREE SYMPATRIC BOWERBIRDS IN AUSTRALIAN WET TROPICS UPLAND RAINFOREST

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Spotted Catbirds *Ailuroedus melanotis*, Tooth-billed Bowerbirds *Scenopoeetes dentirostris* and Golden Bowerbirds *Prionodura newtoniana* were individually marked, measured and examined for moult in upland tropical rainforest on the Paluma Range, northern Queensland. Their adult measurements were compared with those of museum specimens. Biometrical data presented provide information on variation in size and weights for each sex and age group in all three species. Adult female Spotted Catbirds and Tooth-billed Bowerbirds had shorter wings and tails than adult males and adult female Spotted Catbirds also had smaller bills than adult males. Golden Bowerbirds were distinctive in that females were the larger-billed sex but had a tail only 81 per cent as long as that of adult males. Bowerbirds lost weight in September–October, at the beginning of their display and breeding season, but gained weight as the season progressed. The overall moult period for all three species was December to March inclusive, the peak moulting months being January to March after display and breeding declined and wet season rains had commenced. Moult of head and body plumage began before that of wing and tail. Immature male Golden Bowerbirds without traditional bowers began moult during September and November, whereas adult bower-owning males began moulting in late December. Primary moult was most evident during January and March and finished, or nearly did so, by April. It started in the mid-wing, with the innermost primary, progressing outwards from the body in both wings simultaneously. Secondary moult was most evident during February and March and generally began when the first four or five new primaries were fully-grown or nearly so. It began at S1 to progress toward the body and simultaneously at S7 away from the body. The central secondaries (S3/4–6) were thus replaced last. Tail moult usually started during early stages of primary moult, beginning with the central pair and progressing outwards. It was finished before primary moult and was most evident during February and March. The timing of annual moult relative to other aspects of the life histories of these bowerbirds is discussed. Estimated mean annual survival rate and expectancy of further life after banding was respectively: 72 per cent and 3 years for Spotted Catbirds (both sexes); 90 per cent and 9.4 years for Tooth-billed Bowerbirds (males only) and 91 per cent and 10.9 years for Golden Bowerbirds (males only). The oldest Spotted Catbird we recorded was aged 19 years and a Tooth-billed and Golden Bowerbird attained 20 and 21 years respectively. Both monogamous (Spotted Catbirds) and polygynous (Tooth-billed and Golden) bowerbirds proved to be remarkably long-lived, their high survival rates being briefly discussed in the context of the southern hemisphere and Australian passerine avifaunas.

INTRODUCTION

Twenty bowerbird species form the avian passerine family Ptilonorhynchidae of the Corvinae. Bowerbirds are medium-sized, stocky, strong-legged and -footed, stout-billed birds. Eight are endemic to Australia, ten endemic to New Guinea and two occur in both areas (Sibley and Ahlquist 1990; Frith and Frith 2001a). Seventeen of the 20 species are known or presumed to breed polygynously, in which promiscuous adult males maintain a cleared 'court' or build a 'bower' structure decorated with various objects. Males of most species advertise their court or bower location vocally, defend its site from rival males and, in the case of reproductively successful individuals, mate with several to numerous females each season. Females build and attend the nest alone, unaided by males. The remaining three species are the monogamous catbirds *Ailuroedus* spp. that form pairs for one or more breeding seasons and defend all purpose territories in which they share in the provisioning of offspring (Gilliard 1969; Donaghey 1981, 1996; Donaghey *et al.* 1985; Frith and Frith 2001b).

Four bowerbird species occur sympatrically in upland rainforest of the Australian Wet Tropics of the Atherton Region, northern Queensland: the Spotted Catbird *A. melanotis,* Tooth-billed Bowerbird *Scenopoeetes dentirostris*, Golden Bowerbird *Prionodura newtoniana*, and Satin Bowerbird *Ptilonorhynchus violaceus*. In August 1978 we started long-term studies on the first three species on the Paluma Range, 80 kilometres north of Townsville (Frith and Frith 1985a, 1993, 1994, 1995, 1998, 1999, 2000a,b,c,d, 2001a,b and references therein; Frith *et al.* 1994). Moult in bowerbirds is almost unknown except for the Satin Bowerbird (Vellenga 1980). Bowerbirds have been noted to be distinctive in having a larger number of secondaries (including the tertials) than most passerine birds, the catbirds (*Ailuroedus* spp.), Tooth-billed Bowerbird *S. dentirostris* and maypole builders (*Amblyornis* spp., *Archboldia* and *Prionodura*) having 11–12, and the avenue bower builders (*Sericulus* spp., *Ptilonorhynchus* and *Chlamydera* spp.) having 12–14 (Schodde and Mason 1999; Frith and Frith, pers. obs.). As the moult of tertials is typically not synchronized with the progression of moult across the secondaries in passerines (Ginn and Melville 1983; Jenni and Winkler 1994), the distinction between the two groups of wing feathers is warranted (although they are notoriously difficult to differentiate in many taxa). We assume seven secondaries and at least four tertials in the bowerbird species we studied but stress this awaits detailed anatomical studies to confirm it. Vellenga (1980) recorded Satin Bowerbird moult in ten secondaries, presumably therefore including the three outermost, or largest, tertials.

Our field studies predominantly involved the display and breeding months of late August to early January, from 1978 to 1989, mostly being carried out during 1978 and 1983. This contribution presents and discusses the first data sets for little known aspects of morphology, biometrics, and moult, in all three species studied and longevity and survival rates for Spotted Catbirds. It also updates longevity and survival rates for Tooth-billed and Golden Bowerbirds previously published by Anon (1991) and Frith and Frith (1995, 2000d). Our recording of longevity and survival data continued until November 1999.

During a study tour of collections of bird skins in museums around the world we measured all sexed bowerbird specimens with recorded localities, the resulting morphological and biometrical data for which is presented elsewhere (Frith and Frith 2001a). Here we compare biometrical data from live birds with those from museum specimens of Australian bowerbirds if they differ from, or add significantly to, the former.

STUDY SITE

This study was carried out in upland rainforest, at an altitude of *c.* 850–950 metres above sea level, on the Paluma Range in tropical north-eastern Queensland, *c.* 80 kilometres north of Townsville. This forest is classified as Simple Notophyll Vine Forest (Tracey 1982). Climbing lawyer palms, *Calamus* spp., terrestrial ferns, saplings, and seedlings dominated the understorey. Medium-sized woody lianas and climbing pandans, *Freycinetia* spp., were common. Annual rainfall and temperatures show marked seasonality on the Paluma Range, the dry season extending from April to November, with June to August the driest and coldest months. Rainfall and temperatures increase during September–October and decrease during April–May. Mean monthly maximum temperatures from August 1978 to April 1981 ranged from 16.7°C (July 1979) to 26.6°C (March 1979) and minima from 9.6°C (July 1979) to 19.8°C (February 1981). The hotter wet season is December–March, with most rain falling January–February (see Fig. 1a).

Our study site (19°00'S, 146°10'E) was located 7 kilometres from the township of Paluma and consisted of two 50 hectare plots each measuring 1 x 0.5 kilometres. One of the plots, our main study site and where most mist-netting was carried out, was marked with a grid of metal stakes. The other area was contiguous with the first, extending north westwards up a hill to *c.* 950 metres above sea level (see Frith and Frith 2000a). We also mist-netted randomly, near bowers and nests, in extralimital adjacent areas.

METHODS

We performed a standardized mist-netting programme within the study area. Bowerbirds were mostly caught during the display and breeding seasons (late August/September to December/early January) of 1978 to 1990, 1995 and 1997 and also during some other months of the year in 1979–1984, for a total of 2 523 hours. Results of a long-term banding study of the general rainforest avifauna, including details of net sites, net hours and capture rates, will appear elsewhere (Frith and Frith, unpubl. data). Many bowerbirds were caught during this programme, as well as at other times, at or near Tooth-billed Bowerbird courts (Frith and Frith 1994, 1995), Golden Bowerbird bowers (Frith and Frith 2000b,c,d) and nests (Frith and Frith 1998) and Spotted Catbird nests (Frith and Frith 2001b). We also randomly mist netted Spotted Catbirds in Paluma Township (19°00'S, 146°13'E), mostly during the non-breeding season months of May–August (1978–1982). Most data were collected in our study site, indicated as 'SS' in text, with those from the Paluma Township being indicated as 'PT' in the text.

Each captured bird was banded with an ABBBS metal band and a unique two colour-band combination (= marked). For each bird caught we recorded weight with a Pesola balance to 0.1 gram degree of precision and measured the length of wing (maximum flattened and straightened on a stopped ruler) and tail (from point of entry into skin of longest, central, feather to its tip) with an un-stopped ruler. Total head length (THL) was taken as the maximum distance from bill tip to back of skull and tarsus from the depression in the angle of the intertarsal joint to the distal end of the tarsometatarsus, measured with steel vernier calipers graduated to 0.1 millimetres. Bill length, from union of bill and fore skull (cranio-maxillary hinge) to the upper mandible tip, bill width and depth (at anterior margin of nostril) were also recorded (Rogers in Lowe 1989). Bill length proportionate to both wing length and tarsus length were used as indicators of body size (Andersson and Andersson 1994; Frith and Frith 1997).

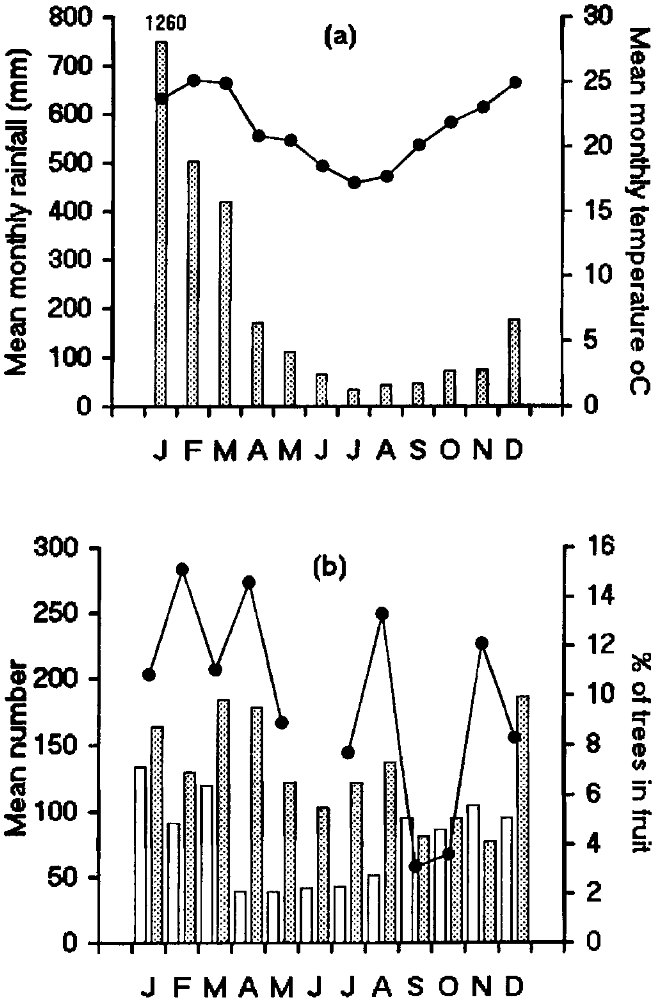

Figure 1. (a) *mean monthly rainfall (columns) and mean monthly maximum temperatures* (•), *and* (b) *mean monthly numbers of diurnal insect (blank columns), forest floor litter invertebrates (stippled columns) and per cent of trees sampled monthly bearing fruits* (•) *summarized for August 1978* to *February 1981, in the study site.*

Biometric data are presented for each species and for each sex and age group of a species where plumage or soft part differences were distinguishable. Juveniles are excluded as very few were examined or measured. In the sexually dimorphic Golden Bowerbird 'female-plumaged' may refer to females or sexually immature males whose plumage is identical to that of females and is thus termed the 'first adult plumage' (Marchant and Higgins 1990), and 'sub-adult' refers to males intermediate between immature and adult male plumage (i.e. trace to almost complete adult male plumage intruding into female-type plumage; Frith and Frith 2000c,d, 2001a). For the sexually monomorphic Tooth-billed Bowerbird we refer to a male as immature if he had pale mouth pigmentation (see Frith and Frith 1995). Weights of sexed specimens of the Spotted Catbird subspecies *A. m. maculosus* (n = 33) were noted from museum specimen labels. As these are mostly for winter months, for which we obtained few weights from live birds, we present them for comparative purposes.

Band colours were subsequently confirmed by direct observation (usually from hides) at bowers and nests to avoid retrapping. Because of this we rarely recaptured a bowerbird subsequently (and then not more than once a season) unless, as in the case of male Goldens, the plumage had changed from an immature (female-like) to an adult one. Only weight, wing and tail lengths, moult and fat levels (see below) were recorded for recaptures. Weights and measurements of recaptures, taken once only during some seasons subsequent to that of original capture are included in statistical comparsions as means and standard deviations proved near identical whether these data were excluded or not. Thus their inclusion does not bias the results in any way. Student's *t*-tests were used for statistical comparisons. Means are given ± one standard deviation.

Fat deposits were subjectively scored on a scale of: 1 (clavicular pit concave and devoid of fat), 2 (clavicular pit covered with fat, its surface slightly concave), 3 (clavicular pit covered with fat, its surface horizontal) and 4 (clavicular pit filled with fat, its surface convex), see Rogers (in Lowe 1989). We refer to these measures of relative fat herein as small (scale 2 of above), medium (3) and large (4) fat deposits.

Moult in wing and tail was scored conventionally from 0 (= old) to 5 (= newly full grown) for each feather, with intermediate scores according to growth (Rogers in Lowe 1989). In most cases we examined the moult in one (usually the right) wing, involving ten primaries (P1 outwards from the body, to P10), seven secondaries (S1 inwards to the body, to S7) and only the two largest tertials (T1 inwards to the body, to T2). Each wing had a potential maximum moult score of 50 for the primaries and 45 for the secondaries including the two larger tertials. All 12 rectrices were examined (R1 central — R6 outermost on left and right side), these having a potential maximum moult score of 60. For wing covert and body moult we used the conventional notations: 0 = no moult, S = slight moult, A = active moult, C = moult completed (Rogers in Lowe 1989). To assess seasonal differences of wing covert and head and body moult between different age groups, sexes and species, and to graphically illustrate them, we subsequently converted these notations to: 0 = no moult, 1 = slight, 2 = active, 3 = completed moult. Wing coverts (primary, secondary, median, lesser, underwing coverts and alula) had a maximum moult score of 18. Five head (crown, forehead, ear coverts, malar region and chin), five upper body (nape, mantle, rump, scapulars and upper tail coverts), and five under body (throat, breast, belly, flanks, under tail coverts) regions were examined for body moult, with a potential maximum total moult score of 45. In the results we present primary moult first, followed by secondary and tertial, wing covert, tail, head, and body moult.

Survival rate was based on resightings and recaptures and calculated from date of initial capture. An estimate of survival rate was obtained by calculating the percentage of individuals known to be alive (by resightings or recaptures) at yearly intervals from the date of their original capture (Nicholls and Woinarski 1988). From mean annual survival we calculated further life expectancy (after Fry 1980).

To avoid complex concluding discussion, biometrics and other aspects of each species are briefly discussed and previous findings referred to, if pertinent, within Results below. To save space, Spotted(s), Tooth-bill(s), Golden(s) etc. are used to refer to the Spotted Catbird, Tooth-billed Bowerbird and Golden Bowerbird respectively where appropriate. The term 'captures' refers to all birds caught, including recaptures, but excludes birds retrapped on the same day that they were captured. The main discussion thus deals only with general comparative aspects of moult and survival.

In the main discussion we relate the seasonality of moult to breeding and emphasize the ecological factors of climate and availability of fruit and animal foods that influence weight, fat deposition and timing of moult. We obtained tree fruiting data from 602 individually marked trees during September 1978 to April 1979, and thereafter from *c.* 500 of them at six- (July 1979 to August 1980) or eight-weekly (November 1980 to February 1981) intervals (Fig. 1b). Diurnal insect populations were monitored each month during July 1979 to February 1981 using Malaise traps (Frith and Frith 1985b). Forest floor invertebrate populations were monitored each month from ridge and gully litter sites during August 1979 to February 1981 (Fig. 1b; D. Frith and C. Frith 1990).

RESULTS

Captures and biometrics

SPOTTED CATBIRD

A total of 118 individual Spotteds were marked: 16 adult males (SS), 22 adult females (SS) and 80 unsexed (38 in SS, 42 in PT). We confirmed the sex of the former 38 SS individuals during subsequent observations of them at nests, as only females incubate and brood (Frith and Frith 2001b). Thirty-four marked individuals were recaptured: 24 once, 9 twice, and 1 three times — a total of 45 recaptures. Of the total 163 captures, 104 were in the SS and 59 in PT. Most SS captures (80%) were during the nesting season months September–December (Frith and Frith 2001b).

Biometric data for the 163 captures (118 marked individuals, 45 recaptures) are given in Table 1. Mean tail, tarsus, and bill lengths represented 69, 29 and 23 per cent of mean wing length respectively for all captures. Mean wing and tail lengths of females were shorter, by 4 per cent, than those of males, the difference being significant (wing: $t_{52} = 5.58$, $P < 0.001$; tail: $t_{52} = 4.81$, $P < 0.001$). Female tarsus length was also significantly ($t_{32} = 4.79$, $P < 0.001$) shorter by 6 per cent, than males. Bill length proportionate to wing and tarsus length was 23 and 77 per cent in males and 23 and 79 per cent in females respectively, thus similar between the sexes. Females weighed significantly ($t_{57} = 3.71$, $P < 0.001$) lighter by 7 per cent, than males.

During the course of another study we measured 57 adult male and 36 adult female Spotted Catbird museum skins of the Australian subspecies *A. m. maculosus* (see Introduction). Resulting measurements were similar to those obtained from live birds, with females smaller than males in every trait (Table 1, this study; Table 3 in Frith and Frith 2001a). Wing and tail measurements of museum skins were slightly smaller (<4%) than those of live birds, presumably due to the shrinkage of the dried skin.

There was a considerable difference between average weights of SS and PT Spotteds (Table 1). The 101 SS captures averaged 174 ± 14 grams and were thus 15 per cent lighter than the 59 PT birds that averaged 205 ± 24 grams, this difference being significant ($t_{158} = 9.23$, $P < 0.001$). Such difference in mean weight possibly reflected the time of year, as follows: of the 101 SS captures, 75 per cent were weighed in September–December, 9 per cent in January–April, none in May–July and 16 per cent in August (Fig. 2). Of the 59 PT captures, only 5 per cent were weighed in October–December, 46 per cent in May–July and 49 per cent in August (Fig. 2). Comparing August weights at both localities (SS = 175 ± 14 g, n = 11 versus PT 195 ± 20 g, n = 29) clearly demonstrates the difference between them, however. By comparing weights obtained from museum specimens with weights from our field study this difference was substantiated. Weights from *A. m. maculosus* museum specimens, in averaging 170 ± 15 g (n = 33), are similar to the average weight of SS captures (see above). Twenty-five of the museum specimens were weighed when collected in May–July, and a comparison of their mean weight (171 ± 15 g) with that of the May–July PT captures (219 ± 19 g, n = 27) supports the possibility

TABLE 1

Measurements (mm) and weights (g) of 163 captures of live Spotted Catbirds on the Paluma Range, north Queensland[1].

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight (SS)[2]	Weight (PT)[2]
Male: adult	(16 individuals and 12 recaptures)								
Mean	154	106	45.1	66.0	34.8	10.2	14.5	183	
SD	4.06	2.81	1.55	1.41	1.50	0.54	0.45	11.24	
Min	142	99	41.6	65	31.2	9.5	13.7	157	
Max	164	110	47.4	67	37.2	11.3	15.2	205	
n	22	21	16	2	15	12	12	27	
Female: adult	(22 individuals and 14 recaptures)								
Mean	148	102	42.6	63.8	33.6	9.6	13.5	171	
SD	3.18	3.06	1.42	1.46	1.12	0.27	0.56	13.17	
Min	140	93	40.5	61.8	32.4	9.2	12.8	150	
Max	155	110	45.3	65.1	36.9	10.2	14.5	198	
n	35	34	20	5	18	11	11	36	
All captures	(n = 118 individuals and 45 recaptures)								
Mean	150	104	44.0	64.0	34.2	9.9	14.1	174	205
SD	4.54	3.54	1.72	1.32	1.32	0.46	0.55	13.58	23.64
Min	135	93	39.1	61.2	28	8.7	12.8	145	163
Max	164	111	49.4	67	38.8	11.3	15.3	205	264
n	148	144	106	38	111	88	88	101	59

[1] = all traits not necessarily recorded for all captures.
[2] = weights are for study site (SS) and Paluma Township (PT) captures; see Result.

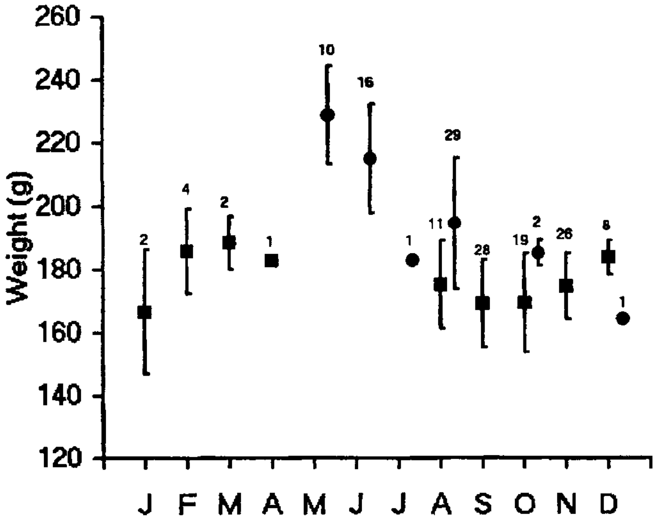

Figure 2. *Monthly mean weights for 101 study site (▪) and 59 Paluma Township (•) Spotted Catbird captures (numbers above symbols = monthly sample sizes, and error bars = standard deviation of the mean).*

that PT birds were indeed the heavier, by 22 per cent, during these months.

The latter weight differences were further emphasized by fat deposit results, those of SS birds being smaller than those at PT. In the SS, 78 per cent of captures had small to medium fat deposits, and 22 per cent no fat. In contrast, 49 per cent of PT Spotteds had large fat deposits, 29 per cent small to medium ones, and 22 per cent no fat (Table 2). In August, when samples for both SS and PT Spotted were large enough to compare (see above), those of SS mostly (55%) had medium sized fat deposits while those at PT were mostly large (44%) or medium (35%). Thus PT Spotteds were heavier with larger fat deposits than birds at the SS seven kilometres away. We believe that this was because of the artificially subsidized diet of PT birds habituating 'bird feeders' to eat food (bread, scones etc.) put out daily by Paluma residents and visitors (pers. obs.).

Average monthly weights fluctuated in the SS samples during the display and breeding season, being low at the start of the season, in September–October, but increasing towards the end of it (Fig. 2). This seasonal weight change was reflected in both breeding adult males and females (Fig. 3). Adult males averaged 186 ± 8 grams in August but 177 ± 14 grams (or 5% less) in September. Similarly, adult females averaged 166 ± 13 grams in August but 158 ± 8 grams (or 5% less) in September (Fig. 3). Weights of both sexes increased in October–December and, although samples were small, were heaviest in February–March (see Figs 2 and 3). Twenty-one captured birds lacked fat during August–February and 13 of them were breeding adults (5 males and 8 females).

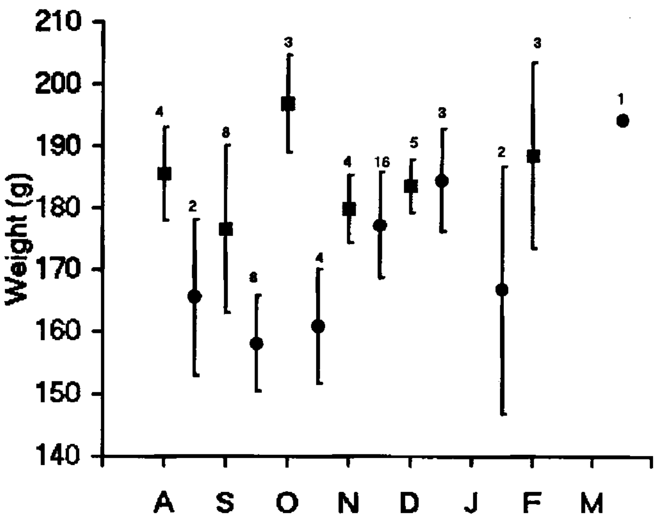

Figure 3. *Monthly mean weights for 27 male (▪) and 36 female (•) Spotted Catbird captures during August–March in the study site. Error bars = standard deviation of the mean.*

TABLE 2

Monthly proportions of levels of fat deposits[1] observed on Spotted Catbirds expressed as a percentage of the monthly sample of captures in the study site and Paluma Township, and of Tooth-billed and Golden Bowerbirds in the study site on the Paluma Range, north Queensland.

	Fat deposit	J	F	M	A	M	J	J	A	S	O	N	D	Total captures
SPOTTED CATBIRD														
Study site	1	100	50						9	8	37	16	42	21
	2		25	50					36	80	48	48	29	49
	3		25	50	100	100			55	12	15	36	29	27
Total captures		2	4	2	1	1	0	0	11	25	19	25	7	97
Paluma Township	1								14		50			13
	2								7		50		100	4
	3						13	100	35					13
	4					100	87		44					29
Total captures		0	0	0	0	10	16	1	29	0	2	0	1	59
TOOTH-BILLED BOWERBIRD														
Study site	1	38								50	54	70	55	35
	2	62							100	40	39	25	45	25
	3			100			100			10	7	5		5
Total captures		8	0	1	0	0	1	0	1	10	13	20	11	65
GOLDEN BOWERBIRD														
Study site	1	45								6	13	14	19	17
	2	55	100	41	67	67	88	33	80	78	78	72	75	112
	3			59	37	37	12	67	20	16	9	14	6	30
Total captures		11	2	17	6	6	8	3	5	32	32	21	16	159

[1] Fat deposit: 1 = no fat; 2 = some; 3 = medium amount; 4 = large amount; see Methods.

TABLE 3

Measurements (mm) and weights (g) of 78 captures of live Tooth-billed Bowerbirds on the Paluma Range, north Queensland[1].

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
Male: adult (n = 29 individuals and 22 recaptures)								
Mean	150	103	32.1	57.9	31.0	10.3	14	157
SD	3.12	1.80	0.99	1.00	0.74	0.33	3.79	8.95
Min	144	100	29.8	56.2	29.8	9.5	12	141
Max	157	107	33.7	59.7	32.2	11.1	33	181
n	41	38	27	15	27	26	26	46
Male: immature (n = 9 individuals and 1 recapture)								
Mean	150	103	31.5	58.7	30.0	10.4	14	164
SD	2.81	1.55	1.81	1.00	1.50	0.31	0.51	12.48
Min	146	101	28.0	57.4	27.2	10.0	13	151
Max	155	106	33.0	59.7	31.4	10.7	15	185
n	10	8	7	5	7	7	7	10
Female (n = 1 individual)								
Mean	147	101	32.1	58.5	31.2	10.4	13.5	182
Unsexed (n = 15 individuals and 1 recapture)								
Mean	148	103	32.0	58.2	31.3	10.4	13	158
SD	4.52	1.88	1.08	0.78	0.95	0.42	0.46	10.70
Min	136	100	29.8	57.6	29.9	9.7	12.5	138
Max	152	106	33.8	59.3	33.4	11.3	14.2	179
n	16	16	15	4	15	15	15	14
All captures (n = 54 individuals and 24 recaptures)								
Mean	149	103	32.0	58.1	30.9	10.4	14	158
SD	3.54	1.77	1.14	0.96	0.99	0.35	2.77	10.32
Min	136	100	28	56.2	27.2	9.5	11.9	138
Max	157	107	33.8	59.7	33.4	11.3	32.5	185
n	68	63	50	25	50	49	49	71

[1] = all traits not necessarily recorded for all captures.

TOOTH-BILLED BOWERBIRD

Fifty-four individuals were marked: 29 adult males, nine immature males, one confirmed female and 15 unsexed. All were marked in the SS except four (a female, a male, and two unsexed) that were measured after they had flown into PT windows. The 29 adult males were long-term owners of traditional court sites (see Frith and Frith 1994, 1995). Fourteen marked individuals were recaptured: 8 once, 2 twice and 4 three times: a total of 24 recaptures. Most Tooth-bills (86%) were mist-netted during the peak display season of September–December, when males were attending (thus the sexing of pale-mouthed immature males), and conspecifics were visiting, traditional court sites (Frith and Frith 1994).

Biometric data for the 78 captures (54 individuals and 24 recaptures) are given in Table 3. Mean tail, tarsus, and bill lengths represented 69, 22 and 21 per cent of mean wing length respectively for all captures; thus the Tooth-bill is a conspicuously short legged bowerbird. There was little difference in size between adult and immature males. Immature males averaged heavier, by 5 per cent, than adults but the difference was not significant (t_{54} = 1.68, P > 0.1). Bill length proportionate to wing and tarsus length was 21 and 97 per cent respectively in adult males and these proportions were the same for the only female.

Skins of 35 adult male and 25 adult female Tooth-bills were examined. Measurements of live adult males (Table 3) were negligibly larger, by 1 millimetre or less, than skins (Table 4 in Frith and Frith 2001a). Measurements of the one confirmed live female were near identical (within 0.5 mm) to the mean figures of 25 female skins. Wing and tail lengths of this one live female were shorter, by 2 per cent, than those of 41 live adult males (see Table 3), but until we examined female skins we could not be sure this was characteristic. Wing and tail lengths of female skins proved, however, to be 2 and 3 per cent smaller than those of males respectively, these differences between the sexes being significant (wing: t_{68} = 3.3, P < 0.01; tail: t_{68} = 4.66, P < 0.001).

The average weight of 71 captures was 158 ± 10 grams Monthly average weight for these is shown in Figure 4. Weights fluctuated during the display/breeding season, decreasing at its commencement, in September–October, but increasing in December–January towards its end. Many captures (38%) had a small fat deposit, and a few (8%) medium-sized ones, but the remainder (54%) lacked fat (Table 2). Those lacking fat included 24 of 41 court-owning adult males examined during September–January.

Seasonal weight loss in October was reflected in both adult and immature males (Fig. 5). Adult males averaged 165 ± 4 grams in September, but decreased in weight, by 6 per cent, in October to average 155 ± 9 grams. Weights remained low in November, but by January had increased to 163 ± 13 grams (Fig. 5). Immature males showed a similar seasonal pattern, but samples were small (Fig. 5). One immature male was notably heavy in March (185 g) and another in June (179 g), but data were too few to determine if weights increased significantly during colder months.

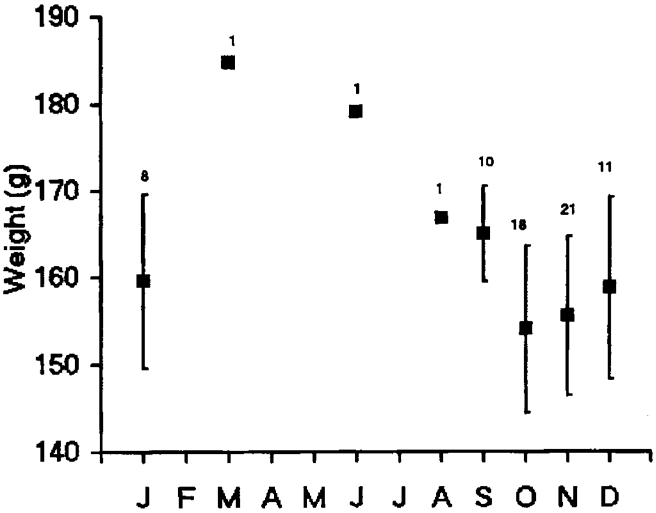

Figure 4. *Monthly mean weights for 71 Tooth-billed Bowerbird captures (numbers above symbols (■) = monthly sample sizes, and error bars = standard deviation of the mean).*

The one confirmed female (a young bird according to her unossified skull) that hit a PT window in November, weighed 182 grams. Her largest oocyte was enlarged to 10 millimetres diameter, suggesting female Tooth-bills may reproduce when relatively young. An adult female with a brood patch, that hit our Atherton Tableland house window, weighed 169 grams and the weight on a December skin specimen, also from the Atherton Tableland, was 157 grams. Thus, three females averaged 171 grams, which is heavier, by 9 per cent, than the average adult male weight of our captures (157 grams, Table 3). Many more female weights are required.

GOLDEN BOWERBIRD

A total 109 individuals were marked in the SS: 36 adult (traditional bower-owning), four sub-adult (i.e. males in female type plumage but with some to much of the yellow adult plumage), and 27 immature males, 12 confirmed females and 30 unsexed female-plumaged birds (Table 4).

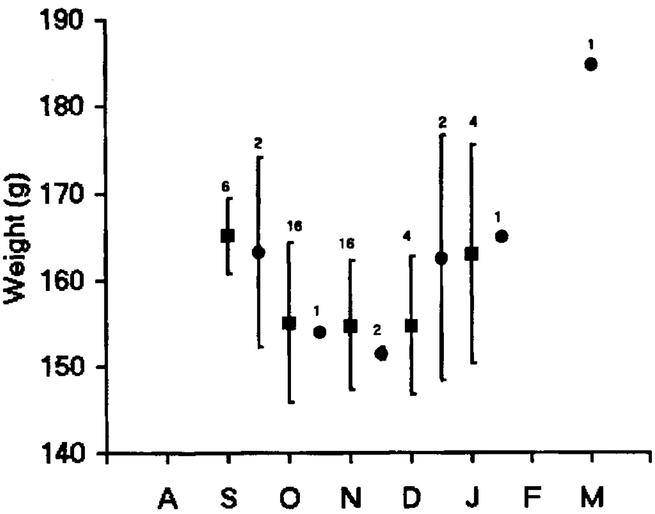

Figure 5. *Monthly mean weights for 46 adult male (■) and 9 immature male (•) Tooth-billed Bowerbird captures during August and March in the study site. Error bars = standard deviation of the mean.*

Thirty-six marked individuals were recaptured: 22 once, 7 twice, 4 three times, 1 four times, 1 six times, and 1 eight times — a total of 66 recaptures. Nineteen of the 31 immature or sub-adult males were subsequently trapped in adult plumage. The period of time individuals wore immature/sub-adult plumage before acquiring adult plumage (>6 years) is discussed elsewhere (Frith and Frith 2000d). Most captures (65%) were during peak display season months, of September–December, when adult males were attending, and other conspecifics were visiting, traditional bower sites (Frith and Frith 2000b,c,d).

Biometric data for the 175 captures (109 marked individuals and 66 recaptures) are given in Table 4. Mean tail, tarsus, and bill lengths represented 82, 26 and 20 per cent of mean wing length respectively for all captures. The relatively long tail of adult males is responsible for the proportionately large tail in this species (see below). Adult females were smaller than adult males in wing and tail lengths but had larger bills and were heavier. Mean female wing length was significantly (t_{84} = 5.23, P < 0.001) shorter, by 3 per cent, than that of adult males. Mean female tail length was significantly (t_{195} = 41.46, P < 0.001) shorter, by 19 per cent, than that of adult males. Tail length of immature/subadult males was similar to that of females (see Table 4), and thus significantly shorter than those of adult males (P < 0.001). Their central pair of tail feathers averaged 14 millimetres shorter than outer tail feathers in adult males, but only 2–3 millimetres shorter in females and younger males. Mean tail length was 90 per cent that of mean wing length in adult males, 71 per cent in immature males and 75 per cent in females. Tarsal and total head lengths were similar in birds of all ages and between the sexes (Table 4). The bill of females was larger in every respect than that of males of all ages, the differences being significant between adult males and females (bill length: t_{47} = 3.46, P < 0.001; bill width: t_{43} = 3.68, P < 0.001, bill depth: t_{43} = 2.79, P < 0.01). Bill length proportionate to wing and tarsus length was 19 and 76 per cent in adult males and 21 and 80 per cent in adult females respectively, thus being slightly larger in females. Adult females were significantly (t_{89} = 6.53, P < 0.001) heavier, by 14 per cent, than adult males, while immature/subadult male weights were similar to those of adult males (Table 4).

TABLE 4

Measurements (mm) and weights (g) of 175 captures of live Golden Bowerbirds on the Paluma Range, north Queensland[1].

	Wing length	Tail length	Tail centrals length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
Male: adult (n = 36 individuals and 47 recaptures)									
Mean	121	109	95	30.7	50.6	23.2	6.4	7.2	73
SD	1.73	2.69	2.06	0.76	0.77	0.52	0.44	0.22	5.10
Min	117	101	87	29.3	49.2	22.3	5.6	6.4	62
Max	125	117	100	32.4	52	24.6	7.9	7.7	86
n	76	75	72	40	33	40	39	39	79
Male: subadult (n = 4 individuals and 3 recaptures)									
Mean	119	87	84	29.6	50.7	23.7	6.6	7.2	71
SD	1.38	4.02	1.51	0.49	0.30	0.58	0.46	0.31	2.67
Min	118	79	82	29	50.3	22.9	6.2	6.7	68
Max	122	91	86	30.1	51.1	24.3	7	7.4	76
n	7	7	7	4	5	4	4	4	7
Male: immature (n = 27 individuals and 15 recaptures)									
Mean	119	88	85	31.0	50.4	23.3	6.5	7.2	75
SD	1.80	1.55	2.08	0.62	0.64	0.58	0.35	0.25	3.77
Min	115	84	78	29.7	49.5	21.3	5.9	6.8	69
Max	124	90	90	32.1	51.5	24.2	7.4	8.1	82
n	40	40	38	27	7	27	28	28	42
Female: adult (n= 12 individuals and 1 recapture)									
Mean	118	88	86	30.8	50.2	24.5	7.2	7.6	85
SD	1.94	1.96	1.22	0.91		1.10	0.39	0.34	6.44
Min	115	85	84	29.4	50.2	23.3	6.8	7.2	76
Max	121	90	88	32	50.2	26	7.9	8.1	96
n	13	12	12	9	1	9	6	6	12
Unsexed (n = 30 individuals)									
Mean	117	87	84	30.6	50.5	23.6	6.9	7.4	76
SD	2.09	1.79	1.82	0.91	0.75	0.62	0.69	0.58	4.37
Min	111	83	81	28.6	49	22.4	6	6.1	69
Max	121	90	88	32.5	52.1	24.7	8.5	8.9	86
n	29	24	24	25	17	25	25	25	29
All capture (n = 109 individuals and 66 recaptures)									
Mean	120	98	89	30.7	50.5	23.5	6.6	7.3	75
SD	2.43	10.84	5.40	0.81	0.71	0.71	0.54	0.38	5.70
Min	111	83	78	28.6	49	21.3	5.6	6.1	62
Max	125	117	100	32.5	52.1	26	8.5	8.9	96
n	165	158	153	105	63	105	102	102	169

[1] = all traits not necessarily recorded for all captures.

We examined 74 adult male and 30 adult female Golden Bowerbird museum skins and found that their measurements were nearly identical (within 1 mm) to those of live birds (Table 4; Table 10 in Frith and Frith 2001a). Our live measurements show females significantly smaller in wing and tail lengths but larger in all bill measurements than adult males. The skin measurements and particularly the much larger bill samples they provided, substantiated this finding. The great difference between adult male and female tail length presumably reflects sexual selection upon males for courtship display attributes (the tail is also brightly coloured), as is dramatically demonstrated within the bird of paradise family Paradisaeidae (Frith and Beehler 1998). Courtship by males involves extensive ritualized flights about the bower, at one to several meters above ground. These flights include the striking rapid and alternating fanning and closing of the tail during a hover display (see Frith and Frith 2000b).

The average weight of 169 captures (sexes combined) was 75 ± 6 grams. Monthly average weights for these birds are shown in Figure 6. Weights fluctuated during the display/breeding season, decreasing at its commencement in September–October and increasing in November–January to reach a peak (mean = 79 ± 3.37 g) in March (Fig. 6). Most captures (70%) had small fat deposits, and a few (19%) a medium-sized one (Table 2). The remaining 17 lacking fat included 13 of 50 bower-owning adult males examined during September–January. Numbers of Goldens lacking fat increased as the display season progressed but fat loads increased from March through the colder months to July (Table 2).

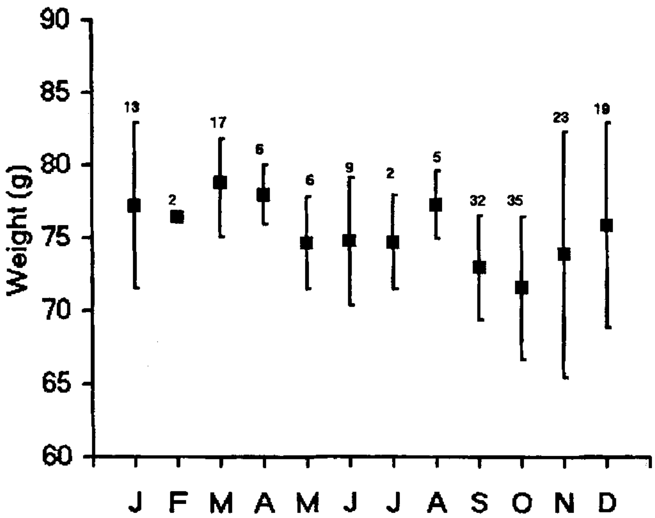

Figure 6. *Monthly mean weights for 169 Golden Bowerbird captures (numbers above symbols (▪) = monthly sample sizes and error bars = standard deviation of the mean).*

Weight loss in September–October was reflected in both adult and younger (sub-adult/immature) males (Fig. 7). Adult males averaged 77 ± 2 grams (n = 5) in August but this figure decreased by 5 per cent in September to 73 ± 4 grams (n = 21). In October it had decreased by another 6 per cent to 69 ± 4 grams (n = 20). Adult males were lightest in November, but by January they had gained weight to 73 ± 3.4 grams and in March to 85 ± 1 grams (Fig. 7). Monthly weights of younger males showed a similar trend to that of adult males with weight loss during the display season (see Fig. 7). Female weight increased during November–December, but monthly sample sizes were too small for meaningful comparisons (Fig. 7).

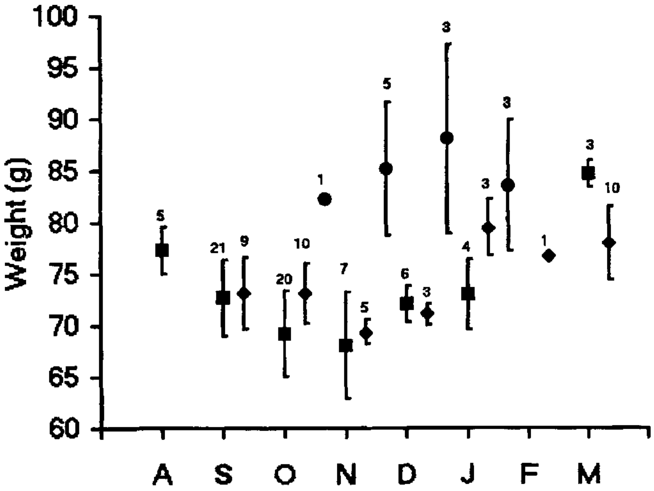

Figure 7. *Monthly mean weights for 66 adult male (▪), 41 subadult/immature male (♦) and 12 adult female (•) Golden Bowerbird captures during August–March in the study site. Error bars = standard deviation of the mean.*

Moult and its seasonality

SPOTTED CATBIRD

Of 139 captures examined for moult, 106 had no moult and 33 had some during some months except July (Table 5). During August–October 13 per cent of birds, including some adult males, had slight head and body moult (see below) but no moult in their wings or tail. During November–December, 50 per cent of birds were moulting in wings, tail, and/or body. During January–April all birds were actively moulting and by May–June moult was nearly complete (Table 5). The rate at which moult proceeded in primaries, secondaries, wing coverts, tail, head and body during November–May (n = 34; see Table 5) is shown graphically in Figure 8. Monthly samples were too small to present sex or age groups separately.

Primary moult started at the end of November and lasted until early May, peaking during January–March (Fig. 8a). In November–December 3 of 14 captures — two females and one unsexed bird — began primary moult but it was not observed in adult males for which samples were small (Table 5, Fig. 8a). Primary moult progressed outwards from the body, beginning with P1 in nine captures and with P2 in two (an adult female and an unsexed bird; Table 6). By February P1–4 were fully-grown, P5–8 partly so, with P9–10 unmoulted (Table 6). By April–May all birds had finished primary moult before finishing secondary moult (see below). The moult sequence progressed simultaneously in both wings in at least four individuals but this was not systematically recorded in others.

Secondary and tertial moult was observed during December–May, peaking during February–March/early April (Table 5, Fig. 8b). Secondary moult began with S1 in all 11 captures (Table 6). In December one female (of five captures) began moulting her S1, her P1–3 being

TABLE 5

Numbers of captures of Spotted Catbirds examined for moult (n = 139) showing moult in each month on the Paluma Range, north Queensland.

	Months (total number of captures)												
	J (2	F 4	M 2	A 1	M 11	J 16	J 1	A 40	S 29	O 21	N 27	D 9)	Total (163)
Adult male													
Examined for moult	0	1	0	0	0	0	0	4	6	3	1	2	17
Wing moult: primary	0	1	0	0	0	0	0	0	0	0	0	0	1
secondary and tertial	0	1	0	0	0	0	0	0	0	0	0	0	1
covert	0	1	0	0	0	0	0	0	0	0	0	0	1
Tail moult	0	1	0	0	0	0	0	0	0	0	0	0	1
Body moult	0	1	0	0	0	0	0	0	2	1	0	1	5
Total with some moult	0	1	0	0	0	0	0	0	2	1	0	1	5
Adult female													
Examined for moult	2	0	1	0	0	1	0	2	8	4	2	2	22
Wing moult: primary	1	0	1	0	0	0	0	0	0	0	1	1	4
secondary and tertial	0	0	1	0	0	0	0	0	0	0	0	1	2
covert	1	0	1	0	0	0	0	0	0	0	0	0	2
Tail moult	1	0	1	0	0	0	0	0	0	0	0	0	2
Body moult	2	0	1	0	0	0	0	0	0	0	1	0	4
Total with some moult	2	0	1	0	0	0	0	0	0	0	1	1	5
Unsexed													
Examined for moult	0	3	1	1	11	15	1	34	14	13	6	1	100
Wing moult: primary	0	3	1	0	1	0	0	0	0	0	1	0	6
secondary and tertial	0	3	1	1	2	0	0	0	0	0	0	0	8
covert	0	3	1	1	1	1	0	0	0	0	1	1	9
Tail moult	0	3	1	0	0	0	0	0	0	0	2	0	6
Body moult	0	3	1	1	2	1	0	4	1	3	1	1	18
Total with some moult	0	3	1	1	5	1	0	4	1	3	3	1	23
All captures: total number													
Examined for moult	2	4	2	1	11	16	1	40	28	20	9	5	139
Total with some moult	2	4	2	1	5	1	0	4	3	4	4	3	33
Per cent with moult	100	100	100	100	46	6	0	10	11	20	44	60	24

TABLE 6

Moult sequence of the primary and secondary feathers (expressed as a % of the potential maximum total moult score per feather[1]) in Spotted Catbirds, Tooth-billed and Golden Bowerbirds, on the Paluma Range, north Queensland.

	SPOTTED CATBIRD								TOOTH-BILLED BOWERBIRD					GOLDEN BOWERBIRD							
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Oct	Nov	Dec	Jan	Mar	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
PRIMARIES																					
10						10	100	98					30		3				35	60	100
9						30	100	100					50		2				62	73	100
8					10	30	100	100			2		70						80	90	100
7					15	40	100	100					90						97	100	100
6		2			45	70	100	100				14	100						100	100	100
5		11		30	70	80	100	100			8	14	100				11	30	100	100	100
4		18	8	40	100	100	100	100				26	100			16	31	100	100	100	100
3		23	20	40	100	100	100	100			4	60	100			44	49	100	100	100	100
2		13	20	40	100	100	100	100		1	20	80	100			80	71	100	100	100	100
1[2]		11	20	10	100	100	100	100		1	36	89	100			82	76	100	100	100	100
Total captures	20	9	5	2	4	2	1	11	14	21	18	7	2	37	24	20	11	2	17	6	6
Per cent with moult	0	22	20	50	100	100	0	9	0	5	56	100	100	0	8	55	91	100	94	100	0
SECONDARIES (1–7) and ADJACENT TERTIALS (1–2)																					
1[2]			20		90	100		100			4	9	80			1	16	100	100	100	100
2					45	100		100			6	3	60					30	93	100	100
3					0	30		100											75	97	100
4					0	100		98								2	2		45	80	97
5					0	100		100	3										9	40	93
6					0	100		98		5			50	4	3	1			7	50	100
7					0	20		100		2			60		3				65	100	100
1					25	100		100		2			60						79	100	100
2					25	100		100					60						80	100	100
Total captures	20	9	5	2	4	1[3]	1[4]	11	14	21	18	7	2	37	24	20	11	2	17	6	6
Per cent with moult	0	0	20	0	100	100	20	18	7	10	11	14	100	3	4	15	50	100	100	100	33

[1] = was estimated by multiplying the total moult score of 5 per feather by the number of captures in moult for each month (see Methods). [2] = mid-wing. [3] = moult score recorded for one of the two individuals with secondary moult. [4] = recorded as near-complete. Note: feathers numbered 1 are those in the mid-wing.

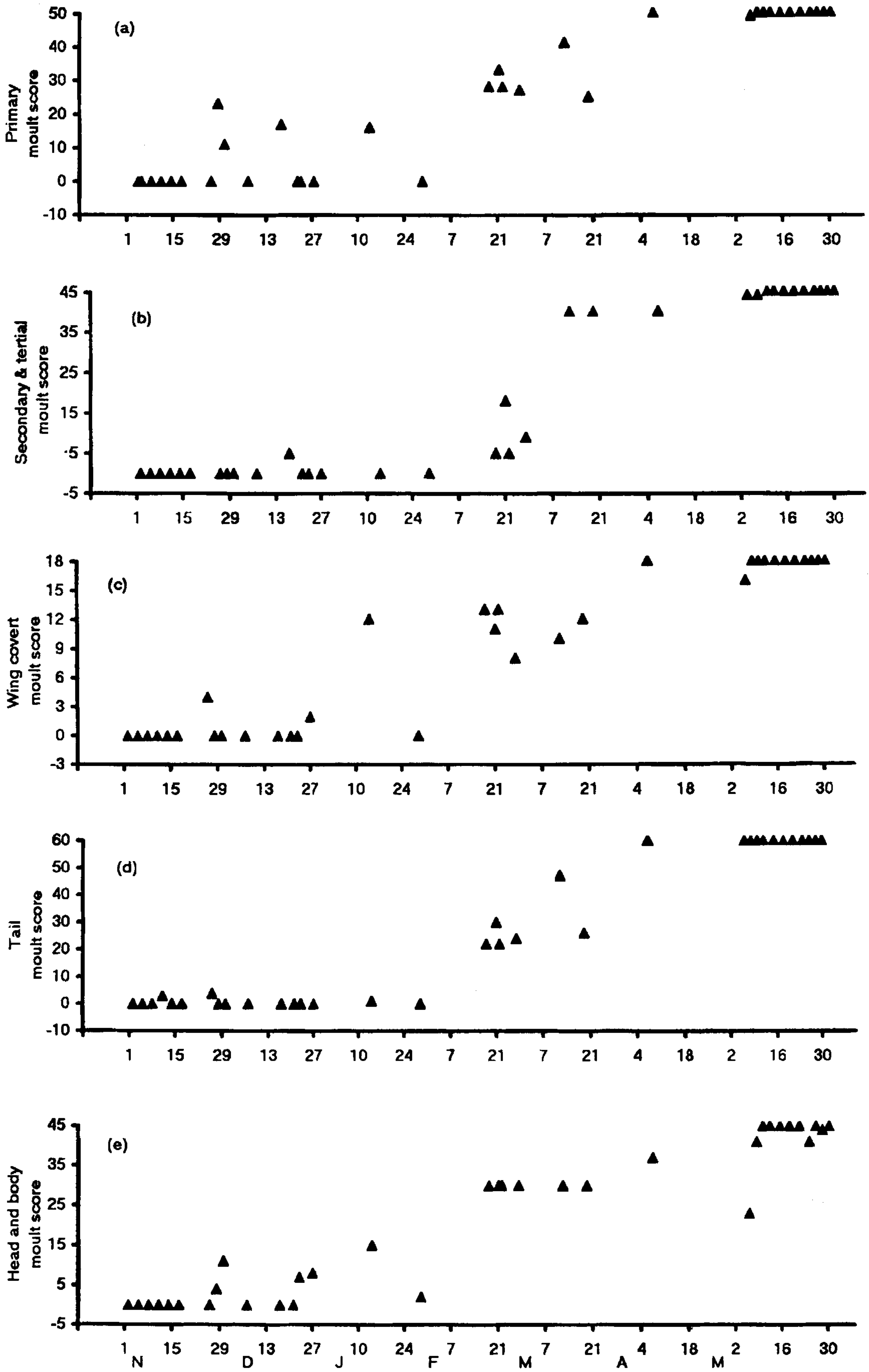

Figure 8. *Moult score for (a) primaries (b) secondaries and tertials (c) wing coverts (d) tail and (e) head and body plumage of Spotted Catbird captures (n = 34) over the peak of moult during November and May; see Methods.*

already newly fully-grown and her P4 partly so. In February four captures had fully-grown S1 and partly grown S2 (one of them also had newly fully-grown T1 and T2); and P1–P4/5 were fully-grown in all of them. Secondary moult finished by May, except the S4 of one capture and the S6 of another. The few data suggest that secondaries moult from S1 inwards and that tertial moult finished before the secondary moult (Table 6). Wing covert moult was noted during November–May, peaking during January–March, when primaries and secondaries were also actively moulting but data were too few to reveal a sequence (Table 5, Fig. 8c). One bird had slight under wing covert moult in May.

Tail moult was most active through late January–early March (Fig. 8d). Two unsexed captures had one partly grown tail feather (left R4 and left R3) as early as November but may have been replacing feathers lost accidentally (Table 7). In the eight birds examined during January–March, tail moult started with the central pair to then progress outwards. In January a female with P1–5 in moult was also growing her two central rectrices. She showed no signs of secondary moult. Four February birds had active tail moult when P1–6 were newly fully-grown or nearly so. This was also the case for two March individuals, except their secondaries were also in moult. Tail moult progressed quickly and finished in April, May and June captures (n = 28), finishing before moult in P9–10 or secondary moult (Tables 5–7).

Head and body feather moult was recorded from August–June, this peaking in January–March (Table 5, Fig. 8e). During August–September, seven (of 68) captures had slight moult in crown, breast, flanks, and/or tail coverts. In October four (of 20) captures had slight moult in the crown, chin, throat, mantle and/or rump. Head moult (crown, forehead, ear coverts, malar, and chin) was most evident during February–March but data were too few to reveal any pattern. One 4 July capture still had slight moult in rump and under tail coverts.

TOOTH-BILLED BOWERBIRD

Of 72 captures examined for moult, 38 had no moult and 34 were moulting, mostly during September–January (Table 8). As most of our data were for adult males, we could not compare moult between sexes or ages. During September–November, 23 per cent of birds showed moult and by December this figure had risen to 78 per cent. All birds were in active wing, tail and body moult during January–March (Table 8). The rate at which moult proceeded in primaries, secondaries, wing coverts, tail, head and body feathering during November–May (n = 48; see Table 8) is shown graphically in Figure 9. Monthly samples were too small to present sex or age groups separately. We did not catch birds in April–May when moult was presumed nearly complete. We have subsequently been able to examine an adult female killed hitting a window at Lake Eacham, Atherton Tableland on 24 May 2000. This bird had finished primary and tail moult, was just nearing the end of secondary replacement, with its S4–6 almost fully grown and the rest newly fully grown and all wing covert moult finished with just a trace of remaining active head and body moult.

Primary moult started in late November, peaking during January–March (Table 8, Fig. 9a). Primary moult began with P1 (n = 20; Table 6). In late November, 1 of 17 adult males caught began primary moult with P1–2 in pin. By December ten captures, including five adult males, had P1–3 partly grown. By January seven birds had their P1–2 almost fully-grown and P3–6 partly so, the rest being old. In March, an immature male had all primaries newly fully-grown except for P9–10 and an unsexed individual was then still growing P7–9 with the old P10 remaining (Table 6). Primary moult progressed sequentially outwards from the body in 17 of the 20 captures but in two others (adult males) P5 began to moult before P3–4. In a third (adult male) P8 began before P2 (Table 6). Primary moult finished before secondary moult (see below). We noted that moult progressed simultaneously in both wings of seven

TABLE 7

Moult sequence (expressed as a % of the potential maximum total moult score per feather[1]) of rectrices of Spotted Catbirds, Tooth-billed Bowerbirds and Golden Bowerbirds on the Paluma Range, north Queensland.

	SPOTTED CATBIRD								TOOTH-BILLED BOWERBIRD					GOLDEN BOWERBIRD							
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Oct	Nov	Dec	Jan	Mar	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
LEFT																					
6					10	20	100	100					40					20	91	100	100
5					15	50	100	100					40			13		20	93	100	100
4		7			20	60	100	100					40					20	99	100	100
3		9			35	70	100	100					40			7		30	100	100	100
2					65	80	100	100				14	50					50	100	100	100
1				10	75	80	100	100	1			14	50			7	13	50	97	100	100
1				10	75	80	100	100				9	50		5		13	50	100	100	100
2					15	80	100	100				3	50					50	100	100	100
3					20	70	100	100					40					50	99	100	100
4					35	60	100	100					40				7	30	99	100	100
5					65	50	100	100				3	40				7	20	97	100	100
6					75	20	100	100				3	40		2		7	10	92	100	100
RIGHT																					
Total captures	20	9	5	2	4	2	1	11	14	21	18	7	2	37	24	20	11	2	17	6	6
Per cent with moult	0	22	0	50	100	100	0	0	1	0	0	30	50	0	13	15	27	100	53	0	0

[1] = was estimated by multiplying the value of 5 per feather by the number of captures in moult for each month (see Methods).

Note: feathers numbered one are the central pair.

TABLE 8

Numbers of captures of Tooth-billed Bowerbirds examined for moult (n = 72) showing moult in each month on the Paluma Range, north Queensland.

	Months (total number of captures)												
	J	F	M	A	M	J	J	A	S	O	N	D	Totals
	(7		2			1		1	8	15	21	23)	(78)
Adult male													
Examined for moult	4								4	13	17	10	48
Wing moult: primary	4								0	0	1	5	10
secondary and tertial	0								0	1	2		
covert	0								1	0	1	1	
Tail moult	1								0	1	0	0	2
Body moult	4								1	2	3	4	14
Total with some moult	4								2	3	3	9	21
Immature male													
Examined for moult	1		1			0		0	2	0	1	2	7
Wing moult: primary	1		1			0		0	0	0	0	2	4
secondary and tertial	0		1			0		0	0	0	0	1	2
covert	1		0			0		0	0	0	0	1	2
Tail moult	0		0			0		0	0	0	0	0	0
Body moult	1		1			0		0	0	0	0	2	4
Total with some moult	1		1			0		0	0	0	0	2	4
Adult female													
Examined for moult											1		1
Wing moult: primary											0		0
secondary and tertial											0		0
covert											0		0
Tail moult											0		0
Body moult											0		0
Total with some moult											0		0
Unsexed													
Examined for moult	2		1			1		1	2	1	2	6	16
Wing moult: primary	2		1			0		0	0	0	0	3	6
secondary and tertial	1		1			0		0	0	0	0	1	3
covert	1		1			0		0	0	0	0	0	2
Tail moult	1		1			0		0	0	0	0	0	2
Body moult	2		1			1		0	1	1	0	2	8
Total with some moult	2		1			1		0	1	1	0	3	9
All captures: total number													
Examined for moult	7		2			1		1	8	14	21	18	72
Total with some moult	7		2			1		0	3	4	3	14	34
Per cent with moult	100		100			100		0	38	29	14	78	47

birds, in two the left wing moult being more advanced than the right but we did not systematically record this in others.

Secondary and tertial moult were recorded during October–March, peaking during February–March/early April, although our data are few (Table 8, Fig. 9b). In October–November three captures were growing one or more new secondaries/tertials (S5 only, S6 only, S6–7 and T1) before primary or tail moult (see Table 6). This seasonally early and irregular replacement (see below) may have been due to accidental feather loss. Secondary moult began with S1 in five other captures after primary moult had begun. Two December birds began moulting S1–2 when P1–2 were already growing; one January capture had begun moult in S1–2 when P1–4 were newly fully-grown and P5–6 partly so; and two March captures had each partly/fully-grown S1–2, S6–7, and T1–2 but old S3–5 when their primary moult was nearly finished. The few data suggest that secondaries moulted from S1 inwards and the innermost secondaries (S6–7) and tertials finished moult before the central (S3–5) secondaries (Table 6). Active wing covert moult was observed in September–June, peaking in December–March when primaries and secondaries were also actively moulting but data were too few to define a sequence (Fig. 9c).

Tail moult occurred during October–March, peaking from late January–early March but data were few (Fig. 9d). One adult male had its left R1 in pin in October but had not begun primary moult. One January capture had its right R5–6 in pin but another January and one March capture had started tail moult at the central pair, to progress outward (Table 7). The March capture had nearly finished tail moult.

Head and body moult usually began before that of wing and tail, occurring during September–June and peaking in December–March (Table 8, Fig. 9e). One unsexed September bird had slight body moult on its head and under parts but had active moult in under tail coverts, mantle and rump. Six adult males had slight head and body moult during September–October. One unsexed June bird had some throat feathers in pin. Insufficient head and body moult was recorded to comprehend a pattern.

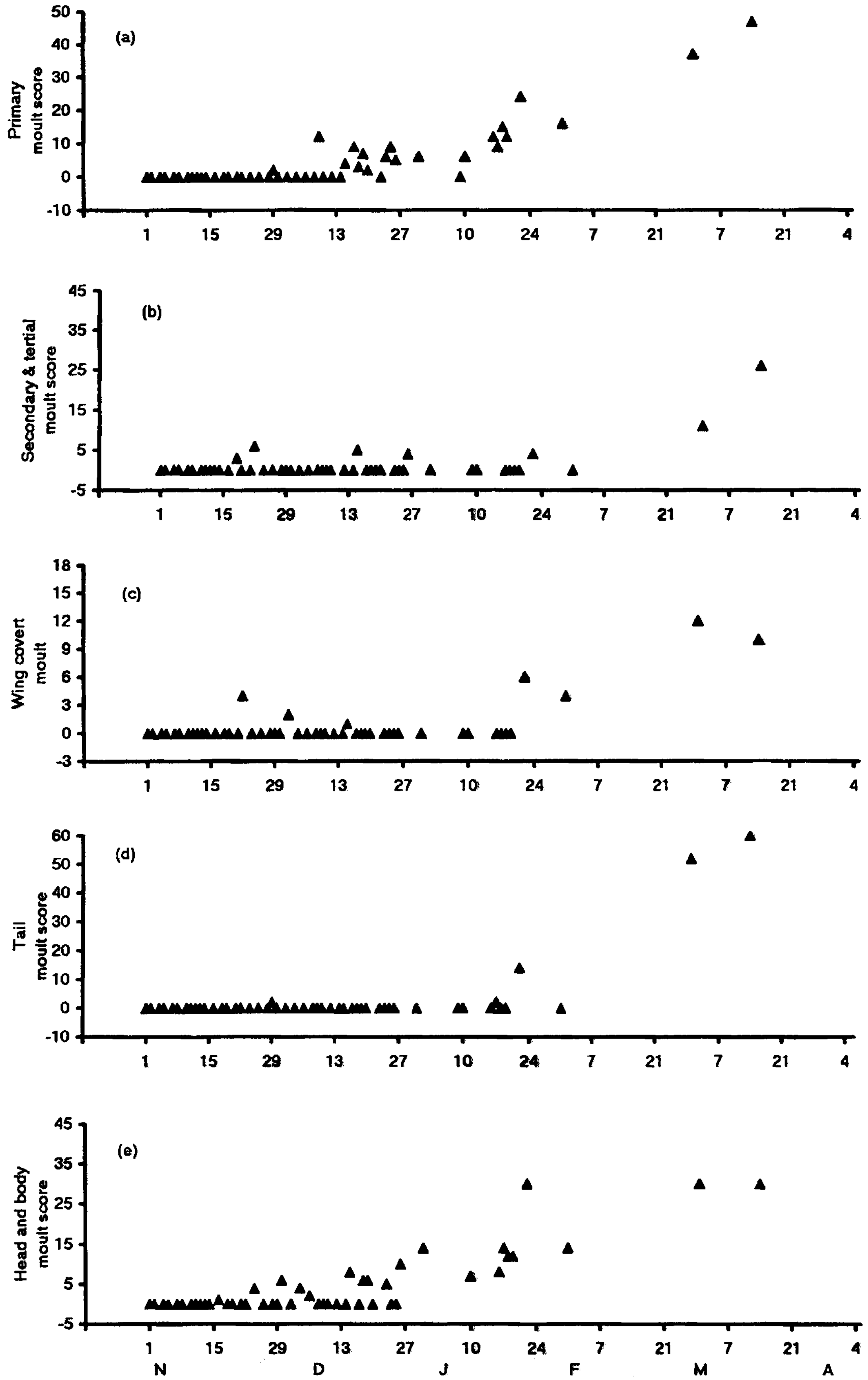

Figure 9. *Moult score for (a) primaries (b) secondaries amd tertials (c) wing coverts (d) tail and (e) head and body plumage of Tooth-billed Bowerbird captures (n = 48) over the peak of moult during November and April; see Methods.*

GOLDEN BOWERBIRD

Of 171 captures examined for moult, 100 had no moult and 71 had some during some months except August (Table 9). In September–November, 29 per cent of 41 female-plumaged captures had started moult in wing, tail and/or body but there was no moult in 52 adult males (see Table 9). Thus limited data suggest female-plumaged birds (including young males) began moulting before adult males. Seventy per cent of December captures, including adult males, began moulting in wing, tail, and/or body. In January most (94%) were actively moulting throughout (Table 9). By May–June most birds had completed moult or very nearly so. The rate at which moult proceeded in primaries, secondaries, wing coverts, tail, head and body during November–May (n = 86; see Table 9) is shown graphically in Figure 10. Monthly samples were too small to present sex or age groups separately.

Primary moult started in November and continued until mid-April, peaking during January–March (Fig. 10a). In two birds (an adult and an immature male), P2 began to moult before P1 but in 44 others moult started with P1 and continued outwards from the body (Table 6). Two of 24 November captures, both immature males, had begun primary wing moult. By December, 11 of 20 captures, including four adult males, had also started primary moult (Table 9, Fig. 10a). By April all primaries except P8–10 were newly fully-grown but by May all were fully new (Table 6). Primary moult was finished before secondary moult (Table 6). We noted the moult sequence to progress simultaneously in both wings in 13 birds but did not systematically record this in others.

Secondary and tertial moult was recorded during October–May, peaking during February–March/early April (Table 9, Fig. 10b). In October an immature male had a partly grown S6 and in November a female had partly grown S6–7, yet neither had primary moult. This seasonally early and irregular replacement may have been due to accidental feather loss (see below). Two December birds also began secondary moult with S4 and S6 but it began with S1 in 33 other captures. Three December and seven January–February captures began secondary moult when their P1–4/5 were newly fully-grown or nearly so (Table 6). The 23 March–April captures clearly showed that secondary moult started at S1 and continued towards S4.

TABLE 9

Numbers of captures of Golden Bowerbirds examined for moult (n = 171) showing moult in each month on the Paluma Range, north Queensland.

	Months (total number of captures)												
	J (13	F 2	M 17	A 6	M 6	J 9	J 2	A 5	S 32	O 37	N 26	D 20)	Totals (175)
Adult male													
Examined for moult	4		3	1	3	7	2	5	21	22	9	6	83
Wing moult: primary	4		2	1	0	0	0	0	0	0	0	4	11
secondary and tertial	1		3	1	1	0	0	0	0	0	0		
covert	4		3	1	0	2	0	0	0	0	0	2	12
Tail moult	1		1	0	0	0	0	0	0	0	0	1	3
Body moult	4		3	1	2	3	1	0	0	0	0	5	19
Total with some moult	4		3	1	2	3	1	0	0	0	0	5	19
Sub-adult/immature male													
Examined for moult	3	1	10	4	2	2			9	10	5	3	49
Wing moult: primary	3	1	10	4	0	0			0	0	2	1	21
secondary and tertial	2	1	10	4	1	0			0	1	0	1	20
covert	2	1	10	3	1	0			0	0	0	0	
Tail moult	0	1	5	0	0	0			1	0	1	0	8
Body moult	2	1	10	4	2	2			0	2	1	0	24
Total with some moult	3	1	10	4	2	2			1	3	3	1	30
Adult female													
Examined for moult	1									1	3	4	9
Wing moult: primary	0									0	0	0	0
secondary and tertial	0									0	1	0	1
covert	0									0	0	0	
Tail moult	0									0	1	2	3
Body moult	0									0	0	0	0
Total with some moult	0									0	2	2	4
Unsexed													
Examined for moult	3	1	4	1	1				2	4	7	7	30
Wing moult: primary	3	1	4	1	0				0	0	0	6	15
secondary and tertial	2	1	4	1	0				0	0	0	2	10
covert	3	1	3	1	0				0	0	0	2	10
Tail moult	2	1	3	0	0				0	0	1	0	7
Body moult	3	1	4	1	0				0	2	0	4	15
Total with some moult	3	1	4	1	0				0	2	1	6	18
All captures: total number													
Examined for moult	11	2	17	6	6	9	2	5	32	37	24	20	171
Total with some moult	10	2	17	6	4	5	1	0	1	5	6	14	71
Per cent with moult	91	100	100	100	67	56	5	0	3	14	25	70	41

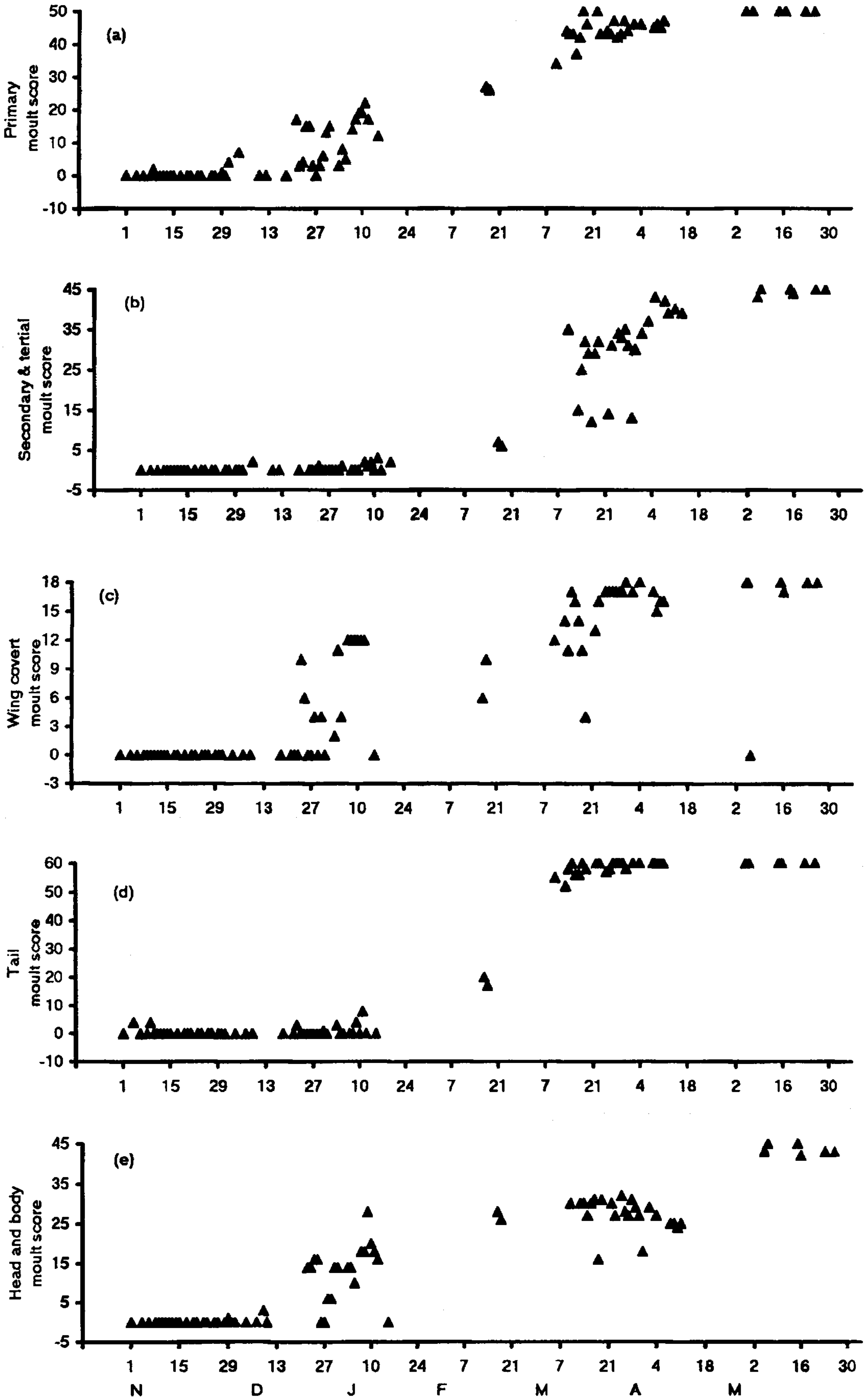

Figure 10. *Moult score for (a) primaries (b) secondaries and tertials (c) wing coverts (d) tail and (e) head and body plumage of Golden Bowerbird captures (n = 86) over the peak of moult during November and May; see Methods.*

Simultaneously (usually when S1–3 were partly grown), moult started in the tertials and also in S7 to progress outwards, with S4–5 being the last replaced in May (Table 6). We did not observe wing covert moult until December (Table 9). It was most active during January–March, when primaries and secondaries were in active moult but data were too few to define a sequence (Fig. 10c).

As for the tail, one immature male had its right R1–2 two-thirds grown in September. Being early, this may have been due to accidental feather loss. Excluding that individual, tail moult started in November, was most active through late January–early March and was complete by April–May (Table 9, Fig. 10d). One female had one partly grown R6 but all 22 other captures started tail moult with the central pair of rectrices, from which it progressed symmetrically outwards (Table 7). Six birds began tail moult in their central rectrices during November–December but only one of these (an adult male) had also begun primary moult, with P1–2 newly fully-grown and P3–4 partly so. Most rectrices were fully grown, or nearly so, by March. Tail moult progressed quickly and finished, or almost finished, before moult ended in P8–10 or in the secondaries (Tables 6 and 7).

Head and body moult took place during October–July peaking during December–March (Fig. 10e). In October–November five female-plumaged captures (three males and two unsexed; see Table 9) had slight moult in under (throat, breast, belly flanks) and upper (nape, mantle, rump, scapulars) parts and/or their crown. We recorded active moult in the under and upper parts of the body in December but only slight moult in the crown. Head moult (crown, forehead, ear coverts, malar, and chin) was most active during February–March. Head and body moult were nearly finished by the end of April and in May–June only a few captures were concluding moult, mostly in some underparts and tail coverts. One adult male had slight upper tail covert moult in early July.

Survival

Calculated mean annual survival rate of 76 SS–marked Spotted Catbirds was 72 per cent (Table 10) and calculated mean expectancy of further life after marking was three years. This brief period of life expectancy was possibly an underestimation resulting from very few marked birds being re-sighted or recaptured by us during the latter part of the study when we spent less time in the field (see Methods). One SS female marked in December 1980 was last re-sighted in October 1989 making her more than 10 years old (i.e. assuming she was a bird of no more than the previous season). An unsexed PT Spotted was last re-sighted in October 1995 wearing only one green band (having lost the other colour). It could have been one of only two birds marked with a band combination including green, in June and October of 1982; thus, this individual was greater than 14 years old. In October 2000 another PT Spotted was re-sighted with only an orange band and could have been one of only four individuals marked with a band combination including orange, in June 1982. Thus it was greater than 19 years old; this and the age of the former individuals, suggested that the estimated expectancy of further life of three years is a gross underestimation.

The mean annual survival rate for 24 adult male Tooth-billed Bowerbirds over 19 seasons (1978–1997) was calculated at 90 per cent, with a mean expectation of further life of 9.4 years (Frith and Frith 2000d). In October 1998 three of the 24 marked individuals were still alive, being greater than 13, 19 and 20 years old. The 19 year old was first marked as an immature (i.e. it then had a pale mouth) as he attended a temporary court (*cf.* Frith and Frith 1995). He became the owner of a nearby traditional court site in season 1983. Thus he was a minimum of four years old prior to owning a traditional site. The 20 year old owned a traditional site when we first marked him, and thus was probably actually greater than 24 years old.

Calculated mean annual survival rate of 48 marked male Golden Bowerbirds during 1978–1997 was 91 per cent, indicating a mean expectancy of further life of 10.9 years (Frith and Frith 2000d). Two adult males were still alive in October 1998, making them greater than 20 and 21 years old (i.e. assuming they were birds of no more than the previous season when marked). A marked adult female was re-sighted only 140 metres from her original point of capture some 14 years after being marked there (Frith and Frith 1998).

TABLE 10

Survival of 76 individually marked Spotted Catbirds over 11 consecutive seasons in the study site on the Paluma Range, north Queensland.

Season	Number of new birds marked[1]	Season 78	79	80	81	82	83	84	85	86	87	88	89	Totals/ per cent (79–89)
78	15	15	9	9	6	1	0	0	0	0	0	0	0	
79	20			16	6	3	3	0	0	0	0	0	0	
80	20				11	5	5	2	1	1	1	1	1	
81	3					0	0	0	0	0	0	0	0	
82	3						1	1	1	0	0	0	0	
84	11								0	0	0	0	0	
87	4													
Number known to be alive at the start of season	76	15	9	25	23	9	9	3	2	1	1	1	1	99
Number present one season later		9	9	12	9	8	3	2	1	1	1	1		56
Percentage annual survival		60	100	48	39	89	33	67	50	100	100	100		72

[1] = birds marked during January and June were included with previous season survival figures.

DISCUSSION

Moult and its seasonality

Sequences of moult and changes of plumages with increasing age are little known in bowerbirds, save for Satin Bowerbirds (Vellenga 1980). In most oscine passerines, primary moult starts with P1 and progresses outwards from the body (Ginn and Melville 1983; Jenni and Winkler 1994). Bowerbirds comply with this rule, primary moult following this sequence in most Spotted Catbirds (9 of 11 captures), Tooth-billed Bowerbirds (17 of 20) and Golden Bowerbirds (44 of 46). Vellenga (1980) described this sequence in Satin Bowerbirds and, like us, found a few irregularities. She noted that such irregularities occurred in some first year birds with worn plumage and in breeding females. We could not be sure what caused the irregularities we observed, though some are probably attributable to accidental feather loss. Two adult female Spotted Catbirds started primary moult early in the exceptionally dry 1979 season, when most nests had failed (see Frith and Frith 2001b). Six Great Bowerbirds *Chlamydera nuchalis* that we examined for moult during October–November in Townsville and ten Spotted Bowerbirds *C. maculata* in November and January south of Charters Towers, all commenced primary moult with P1 (Frith and Frith, unpubl. data). In most individuals of the bowerbird species we have examined, moult progressed simultaneously in both wings but we did not record this systematically.

Primary moult in the three bowerbird species we studied at Paluma began during November but peaked during January–March. It was finished, or nearly so, by April–May. Immature (female plumaged) male Golden Bowerbirds began moult in wing, tail and/or body during September–November but adult males did not do so until late December (Table 9). Our data were too few to determine whether younger, non-bower owning, Golden Bowerbird males finished moulting before adults. This seems likely, however, as they actively attended traditional bower sites during the post-peak display season of March–early May, when the adult males were still finishing primary moult and rarely attended bowers (Frith and Frith 2000b). Primary covert moult usually progressed in the same sequence as their corresponding primaries (*cf.* Ginn and Melville 1983 for passerines in general) but our data were too few for further analysis.

Overall secondary moult peaked in Paluma bowerbirds during February–March/early April, usually beginning after the primaries but with exceptions. Some Tooth-billed and Golden Bowerbirds were growing one, two, or three secondaries early, before either their primary or tail moult or both had begun. This may have involved accidental moult. Most of our bowerbirds did not begin secondary moult until at least their new P1–4/5 were fully-grown, occurring simultaneously in both wings. This appears to be in keeping with other passerines, in which secondary moult begins during the growth of P5 (Jenni and Winkler 1994). Secondary moult in Golden Bowerbirds began with S1 and continued inwards, towards S4 and simultaneously (when S1–3 were partly grown) from S7 outwards. The last secondaries to be changed in May were S4–5 (Table 6). Moult in tertials was finished before that of the secondaries. Spotted Catbird and Tooth-billed Bowerbird data showed a similar pattern of secondary moult (see Table 6). Two Great and five Spotted Bowerbirds commenced secondary moult in S1 but we did not record the secondary moult sequence for these species (Frith and Frith, unpubl. data). Tertial moult began prior to (two Spotted Bowerbirds), or simultaneously with (two Great and four Spotted Bowerbirds), secondary moult. It was noted that secondary moult in the Satin is generally less regular than in the primaries (Vellenga 1980). Secondary moult in Goldens began with S1 and continued inwards, towards S4 and simultaneously (when S1–3 were partly grown) from S7 outwards. The last secondaries to be changed in May were S4–5 (Table 6). In most passerines, secondary moult exclusive of tertials generally commences in the mid-wing with S1 and progresses towards the body, S5–6 thus being the last to be fully replaced (Ginn and Melville 1983; Jenni and Winkler 1994). The latter authors noted that the tertials moult irregularly before moult in the secondaries is finished.

Tail moult usually started during the early stages of primary moult and was finished before P8–10 were fully-grown, as is generally the case in passerines (Ginn and Melville 1983; Jenni and Winkler 1994). It usually began with the central pair of rectrices and progressed simultaneously outwards to each side, as in Satin Bowerbirds (Vellenga 1980). Tail moult commenced during November–December in a few individuals but most birds were in heavy tail moult during February–March. In a few cases one or two rectrices (not always the centrals) were shed before any primaries, possibly as replacements for accidental feather loss.

Our few data suggest that moult in head and body plumage may have started earlier (August) in Spotted Catbirds than in Toothbilled (September) and Golden (October) Bowerbirds. Head feathers are normally the last moulted by passerines (Jenni and Winkler 1994). Head moult began in our bowerbirds before wing or tail moult, peaked during January–March and lasted until June–July or after wing and tail moult was finished. While we noted head moult as being most evident during February–March in Spotted Catbirds and Golden Bowerbirds we did note some slight moult earlier in the season (Tables 5 and 9, Figs 8e and 10e).

Flight and body feather moult occupied the months of December–March inclusive in all three bowerbirds studied at Paluma, given that we could not capture Tooth-billed Bowerbirds after April (see Figs 8–10). It is well documented that many tropical bird species breeding seasonally delay their moult until the end of the reproductive period (Fogden 1972; Snow 1976, 1982; Evans 1985). Peak bowerbird display and breeding months extended from late September–December/early January on the Paluma Range, when temperatures and rainfall seasonally increased and more food (fruit, flying insects & litter invertebrates) became available (Fig. 1; Frith and Frith 1985b; Frith and Frith 1990). Bowerbirds lost weight at the beginning of display and breeding seasons, when fruit was sparse (Fig. 1b) and they were defending territory and nest building (Spotted Catbirds), clearing and decorating courts (male Tooth-billed Bowerbirds) or renovating, building or decorating bowers (male Golden Bowerbirds). As their display and breeding season progressed, food became more abundant and weights of the birds increased. Heavy wet season rains in January–February terminated display and mating activities, with young leaving nests immediately before or during the early wet season (Frith and Frith 1994, 1998, 2000b, 2001b). Moult peaked during the wetter months of January–March, when fruit and invertebrates were most abundant. Towards the end of the moult, weights and fat deposits peaked. Vellenga (1980) also observed that weights in both sexes of Satin Bowerbirds increased after breeding and the completion of moult. Thus moult is fairly synchronized across the species. It was completed and fat deposits were at their greatest, in our study bowerbird species, immediately before the annual lean dry season within their habitat from April–May on (see Fig. 1; Frith and Frith 1985b; Frith and Frith 1990).

The temporal relationship of moult to other major life history events of Spotted Catbirds and Golden Bowerbirds is graphically summarized in Figure 11. The latter events emphasize the observations made above in the context of seasonal relative abundance of various food resources, which are presented in Figure 1. The timing of moult of other rainforest passerines on the Paluma Range followed a similar seasonal pattern (Frith and Frith, unpubl. data), as does moult in some drier Australian habitats (Keast 1968; Crome 1976; Paton 1982). This contrasts with passerines in the Arnhem Land and Kimberley regions where adults tend to moult just prior to the wet season, or delay it till after the wet (J. Matthew, in litt. 10 Nov. 2000). The timing of the annual moult relative (prior) to the annually leanest period, in terms of food resources, was also found in a rainforest avifauna near Kutching, Sarawak (Fogden 1972). In the land avifauna of Trinidad it was found that the timing of annual moult was more predictable than breeding seasonality; thus it has been argued that a few records of moult are a better guide to the breeding season than the same number of breeding records (Snow 1976).

In two manakins (Pipridae) on Trinidad Island, West Indies, and some cotingas (Cotingidae) of the neotropics it was observed that young start their first full (unspecified)

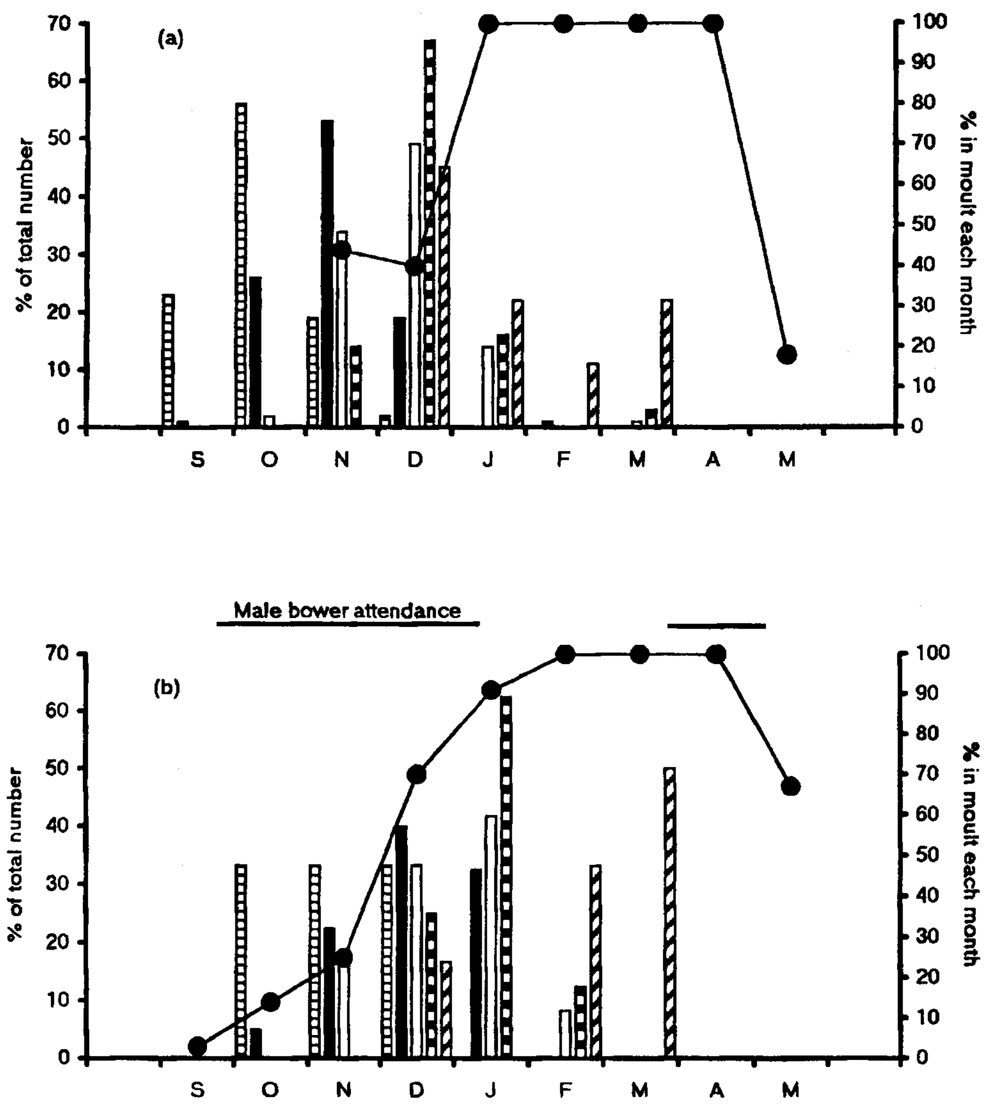

Figure 11. *Per cent (•) of total monthly Spotted Catbird (a) and Golden Bowerbird (b) captures in active moult (for primary moult only see Table 6) relative to percentages of various aspects of their life histories (columns) each month as follows: columns with horizontal lines = nests under construction, black = nests containing egg(s), blank = nests containing nestling(s), horizontal black banding = nests with fledglings departing them, diagonal barring = parent(s) seen with dependant offspring.*

moult at an average of one to two months earlier than subsequent annual moults (Snow 1976). It was also found in some polygynous neotropical passerines that females, on average, begin moult later than males (Snow 1976). In his studies of moult in the cotingas, Snow (1976, 1982) concluded that males in species which have no nesting duties begin to moult early and in species in which the sexes share nesting duties, males moult at about the same time as females. Our bowerbird data are too few but they suggest that males of the monogamus Spotted Catbird may start to moult a little before females; even so, this could be an artifact of the small samples involved (Table 5). We cannot make similar observations, however, on the moult of the polygynously-breeding Tooth-billed and Golden Bowerbirds because our samples are almost exclusively of males. Data for the latter species do suggest, however, that younger males start their annual moult earlier than older males (Tables 9). This may be influenced by the possibility of first year birds moulting earlier than in their subsequent moults (*cf.* Snow 1976). That immature to sub-adult males start each annual moult earlier than adults may be because they are not part of the potentially reproducing male population.

Survival

High survival rates typify Australian passerine birds living in relatively stable environments with year-round availability of food (Woinarski 1985; Yom-Tov 1987; Karr *et al.* 1990; Yom-Tov *et al.* 1992; Martin 1996). Males of polygynous Satin (Vellenga 1980; Anon 1984, 1992, 1994, 1997, 1998; Marchant 1992), Regent (Disney and Lane 1971; Anon 1984, 1995, 1998; Sindel 1989; Lenz 1999), Tooth-billed (Anon 1991; Frith and Frith 1995, 2000d) and Golden Bowerbirds (Anon 1991; Frith and Frith 2000d) are known to be remarkably long-lived passerines. Figures for male survival of these bowerbirds are higher than those recorded for adults of 22 species of temperate southern hemisphere passerines by Fry (1980) and for 22 species of Australian passerines screened by Rowley and Russell (1991). Longevity is not confined to the polygynous bowerbirds, however. The monogamous catbirds are also long-lived (Anon 1995; Frith and Frith 2001b), as are many smaller passerines living in subtropical and tropical rainforests (Snow and Lill 1974; Anon 1991, 1992, 1993; Rowley and Russell 1991; Yom-Tov *et al.* 1992; Frith and Frith, unpubl. data).

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NOTES ON INTERACTIONS BETWEEN COMMON KOELS AND THEIR HOSTS

Brood parasitism in birds is a reproductive strategy found in about 100 species world-wide (Davies 2000). These species lay all of their eggs in the nests of other species — the hosts — who provide all the necessary incubation and feeding required by the hatchlings. It is believed that adult obligate brood parasites play no role in the raising of their own young (Johnsgard 1997). In a recent review, however, Lorenzana and Sealy (1998) drew attention to 40 international published accounts of brood parasites apparently observed to be feeding young of their own species. These authors concluded that the data remained insufficient to declare whether this provisioning of young was an adaptive strategy or simply a vestigial behaviour of pre-parasitic parental care (see also Kikkawa and Dwyer 1962).

The Common Koel *Eudynamys scolopacea* is cited by Lorenzana and Sealy (1998) as a species in which adults had apparently been observed feeding or remaining close to chicks (e.g. see Campbell 1900; Chisholm and Cayley 1929). In most cases, however, few details of these claims are provided by the original authors, making further assessments difficult. Furthermore, despite recent work on vocalizations and host-parasite interactions in Koels (e.g. Gosper 1997; Maller and Jones 2001), much remains to be investigated (Brooker and Brooker 1989). Although largely anecdotal, we provide the following observations of the Common Koel from the Brisbane area as a contribution to increased understanding of this species.

In 1994, the development of a Koel chick was observed in a Noisy Friarbird's *Philemon corniculatus* nest in a suburban garden. Although the familiar 'Cooee' calls of adults Koels were heard frequently throughout the early weeks of the Noisy Friarbird's breeding season (typically September to November in Brisbane), these calls were heard only occasionally while the chick was in the nest. However, many weeks after the fledgling had left the nest (early February) but was still being attended by the foster parents, there was an obvious recurrence in the 'Cooee' calls of adult Common Koels close to the location of the nest. Although other vocalizations of this species time had been heard during this period (indicating that some adults were present in the area), 'Cooee' calls had not been heard in the area for some time. A recent three-year investigation of Koel vocal behaviour has shown this pattern to be typical for the Brisbane area (see Maller and Jones 2001).

Because almost all potential host species have either finished breeding or have large chicks at this time of the year, the function of this spate of calling appeared to be unrelated to the usual apparent functions of such calls: attracting mates or announcing territorial occupation of an area containing suitable host nests (Johnsgard 1997; Davies 2000). Gosper (1997), on the other hand, reported parasitised Magpie-larks *Grallina cyanoleuca* nesting as late as February in northern New South Wales but does not mention any Koels calls being heard. In Brisbane re-nesting by host species at this time appears rare. We wondered,