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NOTES ON THE MORPHOLOGY AND BIOLOGY OF BOWER'S SHRIKE-THRUSH *Colluricincla boweri*, A SEXUALLY DIMORPHIC SPECIES

CLIFFORD B. FRITH and DAWN W. FRITH

P.O. Box 581, Malanda, Qld. 4885

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Our examination of 56 live Bower's Shrike-thrushes *Colluricincla boweri* during 88 captures and of 25 skin specimens showed the species to be sexually monomorphic in size but dimorphic in plumage, contrary to contemporary literature. Adult females have a pale bill and retain the apparently juvenile characters of a rufous superciliary stripe, pale eye-ring feathers and rufous lores, whereas adult males have no rufous superciliary stripe and have pale greyish lores, grey eye-ring feathers, and a black bill. Fifteen active nests and their sites agree with previous data but we report here the first three egg clutch and note that six eggs measured by us were larger than previous measurements. Published illustrations of this bird are reviewed because they are misleading, have caused confusion, and, in one instance, have clearly illustrated the sexual dimorphism we describe.

INTRODUCTION

Bower's Shrike-thrush is by far the most restricted member of the genus and of the family Pachycephalidae in Australia, being confined to tropical rainforests of the Atherton Region, mostly over 400 m above sea level. It feeds mainly upon arthropods predominantly obtained from foliage, vine tangles, branches and tree trunks, mostly in the subcanopy to the upper canopy (Blakers, Davies and Reilly 1984; D. Frith 1984). Little has been published about this bird in the field (Boles 1988), and a paucity of specimens in any single collection appears to have prevented a satisfactory examination of its external morphology (Galbraith 1974).

Current literature treats Bower's Shrike-thrush as a sexually monomorphic, black-billed species with leaden dark-grey upperparts and face, and cinnamon-rufous underparts with a paler throat and greyish tinge across the upper breast; the throat and upper breast are finely streaked with dark grey. Lores are pale grey, and some individuals have a ring of paler, cinnamon-rufous feathers around the eye, which some authors describe as an immature character (Officer 1969; Macdonald 1973; Pizzey 1980; Reader's Digest 1988; Boles 1988). Only Galbraith (1974) tentatively suggested that these differences in the head and wing plumage and bill colour may indicate sexual dimorphism.

STUDY AREA AND METHODS

This study was carried out in upland tropical rainforest, 875 m above sea level, on the Paluma Range in north Queensland (19°00'S., 146°10'E.), as part of several ornithological/ecological studies of this habitat (Frith 1984; Frith and Frith 1985a, in press, unpub. data). This forest is classified as simple notophyll vine forest (Tracey 1982). Annual rainfall and temperature are markedly seasonal. The hotter wet season extends from December to March (average monthly rainfall 400 mm) and the dry season from April to November. The coldest and driest months are June to August.

Mist netting began in August 1978 and is ongoing. Four nets were erected at each of two of 15 standard netting sites at any one time; two nets measured 9.1 m x 2.74 m and two 12.1 m x 2.74 m, and all were opened to an effective height of 2.7 m. A total of 2 435.5 hours have been spent mist netting at these 15 net sites, mostly with eight nets in use at any one time. The

months, number of nets and periods of netting at each site has varied, far less time being spent at fewer sites from 1985 onwards. Netting was carried out during the warmer, wetter months (August/September to January/February), when most tropical rainforest birds were breeding, although some netting was done during the winter months in 1978 to 1980. Some additional netting at other locations was also carried out within the study area. Full details of net sites and netting periods will be published elsewhere. Bands were provided by the Australian Bird Banding Scheme, CSIRO Division of Wildlife, and the Australian Bird and Bat Banding Schemes, Australian National Parks and Wildlife Service. A total of 88 Bower's Shrike-thrush captures were made of 56 individual birds.

To calculate annual survival rate, we used the method described by Nicholls and Woinarski (1988). For every year (i) on a x-year study, the number of banded birds present (a) and the number still present one year later (b) are calculated. The mean percentage annual survival is then estimated as:

$$100 \left(\sum_{i}^{x=1} b \Big/ \sum_{i}^{x=1} a \right)$$

Standard net sites 1 to 4 were the only ones we used every banding season from 1978 through 1988. Survival rate calculations are, therefore, based on capture-recapture data from these sites only. We captured 24 of the 56 individual birds at these four sites in the 1 264 hours spent netting.

Culmen length (tip to union with skull), total head length (bill plus skull length) and tarsus were measured to 0.1 mm using steel Vernier calipers. Wing and tail measurements were taken with a stopped rule to the nearest whole millimetre, the former being the maximum flattened wing length and the latter being measured from the point of entry of central tail feathers into skin to the tip of the longest tail feather. We noted colours of bill, iris and leg; extent of superciliary eye-stripe; moult; and breeding condition (extent of brood patch on a scale 0–3). As a result of plumage variations noted in captured live birds, we examined specimens at the Museum of Victoria, Australian Museum and Queensland Museum.

RESULTS

Plumage dimorphism

The first two birds netted were in different plumages. One had a black bill, pale greyish lores and grey eye-ring feathers and lacked a superciliary stripe (Fig. 1A), which is the plumage usually described as that of adults. The other bird had slightly paler grey upperparts, a distinct rufous-coloured superciliary stripe from above its grey-buff or dirty whitish lores to just behind the eye-ring of rufous feathering (paler below the eye), and a bill with a dark grey upper mandible and a paler, greyish lower one with a distinctly blue-grey base (Fig. 1B). The leading edge of

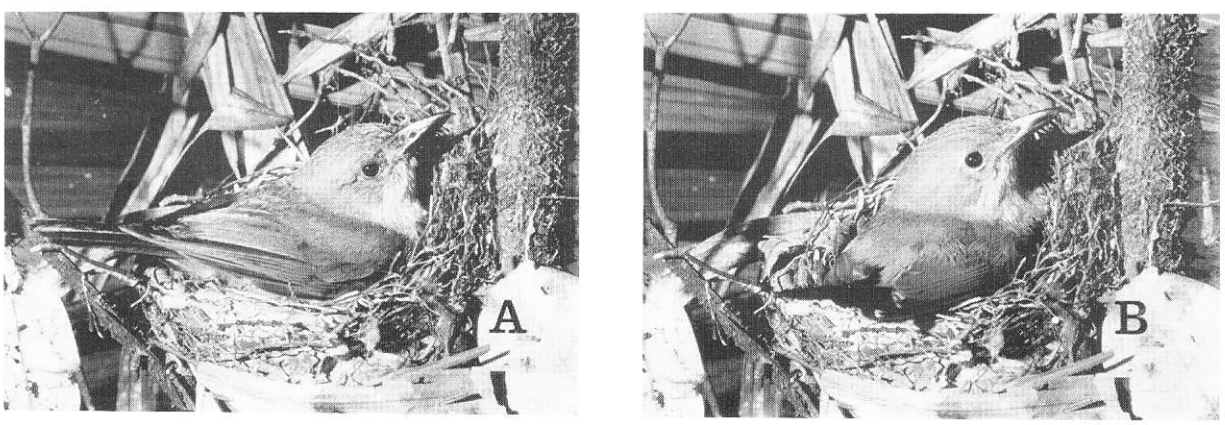

Figure 1. *Male (A) and female (B) Bower's Shrike-thrush incubating on the same nest, at Paluma, Queensland. Note pale eye stripe, lores, and eye ring of the female.*

Photo: C. B. & D. W. Frith

primaries and secondaries in the first bird were rufous-olive and in the second a brighter, more pure rufous. Some of the second bird's characters have apparently been described as, or confused with, immature characters (see Discussion).

We recorded the presence of rufous wing coverts on only three netted birds, which suggests that it was not present in others, but we may have overlooked this character earlier in the study.

During our netting years 1978 to 1980, on five occasions two birds were removed from the same mist net at the same time. In all five instances the two birds of each pair had what we conclude to be adult male and female plumages and soft part colours. At no time were two birds in the same plumage found in the same net at the same time. The five instances of a pair capture were for March (twice) and September (three times), suggesting that the pair-bond probably lasts beyond the breeding season.

TABLE 1

Plumage of skins of Bower's Shrike-thrush in the Museum of Victoria (MV), the Queensland Museum (QM) and the Australian Museum (AM).

Museum	Number	Sex	Eye-stripe	Bill colour
MV	5496	Male	Absent	Black
MV	5497	Male	Absent	Black
MV	5501	Male	Absent	Black
QM	O.5252	Male	Absent	Black
QM	O.14941	Male	Absent	Black
QM	O.14947	Male	Absent	Black
QM	O.14940*	Male	Present	Grey
AM	O.45782	Male	Present	Grey
QM	O.5253	Female	Present	Grey
QM	O.6730	Female	Present	Grey
QM	O.14942	Female	Present	Grey
QM	O.14943*	Female	Present	Grey
QM	O.14945*	Female	Present	Grey
QM	O.14944*	Female	Present	Grey
AM	O.1651	Unsexed	Present	Grey
AM	O.1653	Unsexed	Present	Grey
AM	O.2007	Unsexed	Present	Grey
AM	O.3422	Unsexed	Present	Grey
AM	O.3423†	Unsexed	Present	Grey
QM	O.14956	Unsexed	Present	Grey
AM	O.1648	Unsexed	Absent	Black
AM	O.1650†	Unsexed	Absent	Black
AM	O.1655	Unsexed	Absent	Black
AM	O.1656	Unsexed	Absent	Black
QM	O.11782	Unsexed	Absent	Black

* Has rufous edging on greater wing coverts
† The two skins illustrated by Cayley (1987, p. 171)

Most recent ornithological literature states or implies that the sexes of Bower's Shrike-thrush are alike (Officer 1969; Macdonald 1973; Pizzey 1980; Edden and Boles 1986; Simpson and Day 1986; Slater, Slater and Slater 1986; Boles 1988), although Reader's Digest (1988) pointed out that some birds have a paler ring of feathers around the eye. During photographic work at three different nests, we noted that each pair of nesting birds consisted of a rufous-browed and grey-billed bird and a black-billed one lacking the rufous brow — clearly indicative of sexual dimorphism.

Of the 25 specimens we examined, eight were sexed as male, six as female and 11 were unsexed (Table 1). All females had a rufous superciliary stripe and a grey bill. Six males had no stripe and a black bill, and two males had the female characters of a superciliary stripe and grey bill. Of the two latter skins, AM O.45782 (Table 1) collected at Thornton Peak by W. Boles in 1976 has rufous primary and secondary coverts (W. Boles, pers. comm.), suggesting it is an immature bird, and significantly, the second male skin with female characters (QM O.14940, collected by K. Broadbent in 1889) also has some rufous feathering in its wings. Our measurements of the 12 definitely sexed adult specimens in museums (Table 2) confirm our finding that in live birds the sexes are almost identical in size of all parameters.

Of the 56 live individuals handled, 38 had the superciliary stripe and lighter bill of females (at least 13 of these had a brood patch and were therefore clearly adult females), 14 had a black bill and no superciliary stripe as in males, and four had the black bill of adult males but had either a slight trace of rufous feathering above the eye (two birds) or a distinct superciliary stripe (two birds), and were therefore possibly immature males. One of the latter two was first netted in October 1981, but when retrapped in October 1983 and again in September 1984 had only a very slight rufous wash in the feathers from the nostril back over the eye and the distinct superciliary stripe was no longer present. The four netted presumed immature males had black bills, unlike the two immature male museum specimens with grey bills.

The sexes cannot be separated by the parameters we measured (Table 2). We noted live birds' leg colours as blue-grey, grey or dark grey, and iris colours as red-brown or brown.

TABLE 2

Morphometric data for live Bower's Shrike-thrushes and for sexed museum specimens.

	Adult male pulmage (n=23)	Adult female plumage* (n=28)	All birds netted (n=88)	Specimens Male plumage (n=6)	Specimens Female plumage (n=5)
Weight (g)					
Mean	43.3	44.4	43.5	—	—
SD	3.5	2.7	2.7		
Range	37.0–49.6	37.2–48.6	37.0–49.6		
Number	23	28	84		
Total Head Length (mm)					
Mean	50.7	50.9	50.8	—	—
SD	1.0	1.4	1.6		
Range	50.0–52.2	49.9–51.9	46.3–54.2		
Number	4	2	17		
Bill Length (mm)					
Mean	26.5	26.7	26.5	27.3	27.1
SD	1.1	0.8	1.5	0.8	0.6
Range	25.1–28.6	25.1–28.1	21.2–32.2	26.2–28.0	26.5–27.9
Number	14	13	55	6	5
Wing Length (mm)					
Mean	105.9	106.0	106.2	104.7	104.2
SD	2.1	3.6	2.8	1.0	3.3
Range	102–110	101–113	99–113	103–106	100–109
Number	22	22	77	6	5
Tarsus Length (mm)					
Mean	27.9	28.0	28.3	26.3	26.9
SD	1.1	1.3	1.1	0.7	0.5
Range	25.0–29.3	26.3–31.2	25.0–31.2	25.2–27.0	26.0–27.4
Number	14	13	54	6	5
Tail Length (mm)					
Mean	82.1	82.3	81.9	82.7	81.2
SD	3.5	1.9	2.9	2.6	2.6
Range	76–93	79–86	75–93	79–86	77.84
Number	21	19	70	6	5

*In order to exclude any possibly immature birds these are only those birds found to have a brood patch.

Longevity, survival rates and movements

Of the 56 individuals caught, 22 were recaptured: 15 once, six twice and one five times (second recaptures on the same day are not recorded), a total of 32 recaptures. Fifteen recaptures occurred in the same season as first banding, and eight the following season. Others were recaptured after two years (three birds), three (three), four (one) and five years (one). The longest individual history is that of a female last recaptured exactly seven years after banding at its original banding location.

A summary of capture/recapture data for Sites 1 to 4 is given in Table 3. Of 24 individual birds banded at these four sites, nine were recaptured 14 times in subsequent seasons: nine at Sites 1 to 4, and five at other locations. The estimated mean annual survival rate was 50 per cent (Table 3).

From 1978 to 1988, 32 birds were caught at these four sites during 1 264 hours of netting with eight nets erected, the mean time per bird netted by eight nets being 39.5 hours.

Eleven birds were recaptured at their original capture site while others were retrapped between 50 to 275 m from their original capture site. The (female) bird netted six times (see above) was first caught at site 4 in November 1978, then retrapped in September 1979 at site 1 (175 m from site 4), again in September 1979 at site 15 (88 m

TABLE 3

Capture and recapture of Bower's Shrike-thrush (sites 1 to 4) and survival of birds banded according to year, 1978–1988.

Banding season	Captures (n=24)	Recaptures 79/80	80/81	81/82	82	83/84	84	85	86	87	88
1978/79 (Aug.–Mar.	7	6	0	1	0	0	0	0	0	0	0
1979/80 (Aug.–May)	8		1	0	0	1	0	0	1	0	0
1980/81 (July–Jan.)	2			0	0	0	0	0	0	0	0
1981/82 (Oct.–Jan.)	1				0	1	1	0	0	0	0
1982 (Sept.)	0					0	0	0	0	0	0
1983/84 (Sept.–Mar.)	0						0	0	0	0	0
1984 (Aug.–Sept.)	1							0	0	0	0
1985 (Sept.–Oct.)	1								1	0	0
1986 (Nov.–Dec.)	1									0	1
1987 (Sept.–Oct.)	2										0
1988 (Nov.)	1										
To calculate annual survival rate: No. of recaptures present (a)	14	6	1	1	0	2	1	0	2	0	1
No. of recaptures present 1 year later (b)	7	0	1	0	2	1	0	2	0	1	0

from site 4), in February 1980 at site 10 (275 m distant), in May 1980 at site 4, and in October 1981 again at site 1.

Six of the 14 adult males (43%) netted were recaptured, three of them once only and two twice. Ten of the 13 adult females (77%) caught were later recaptured, eight once only, one twice, and one five times. Only five (20%) of the 25 unsexed female-plumaged birds were retrapped, four of them once and one twice.

Breeding

The nests of Bower's Shrike-thrush found in our study site contained eggs or young from October to January inclusive. CBF observed pair-formation/pre-copulation display on two occasions during September 1978, prior to our appreciating the differences between the sexes. On the first occasion a pair was seen 0–2 m above the forest floor. The apparent male was perched close to the female with its fluttering wings lowered or drooped and tail raised to *c.* 50° but not fanned, while giving the typical Bower's Shrike-thrush 'tuck' note followed by clear whistling song. The male followed the female about displaying in this manner. The second time a bird (presumed male) was seen hopping from perch to perch after a presumed female giving the wing-fluttering display and soft sub-song calls.

We netted 13 female-plumaged birds with brood patches and one male with a possible trace of one. Although this suggests females do most of the incubating, we have observed and photographed both females and males incubating eggs and brooding young at several nests (Fig. 1). We have insufficient data, however, to indicate how nest duties are proportioned between the sexes. Birds were in breeding condition during September (3.6% of those examined had a brood patch), November (46.7%), December (38.5%) and January (20%).

The 15 active nests we examined were 2–9 m high, and built in a sapling fork, among a vine tangle including *Calamus*, or actually on a *Calamus* stem. We saw a pair nest-building in October, and found nests with two eggs in October (two nests), November (five nests) and December (one nest) and with three eggs in January (one nest, perhaps a second clutch). Of six eggs measured, mean length was 28.2 (SD 1.1) mm, mean width 20.8 (SD 0.8) mm and mean weight 6.4 (SD 0.9) g.

Nestlings were recorded in nests during November (four nests), December (two nests) and January (four nests). In January we saw a pair feeding one fledgling, and a single unsexed parent feeding a fledgling larger than itself that was more sandy coloured on the breast than the parent. In February we saw an adult-sized fledgling with a superciliary eye-stripe feeding itself as well as begging for food from its parent.

On 28 December 1978 CBF found a Bower's Shrike-thrush nest 3 m high and approximately 45 m from the nest of a Spotted Catbird *Ailuroedus melanotis* containing a single young catbird with flight feathers in pin. The former nest contained the neatly decapitated body of a nestling of near-fledgling age, and had doubtless been thus mutilated by the adult catbirds, as this is typical of their nest predation behaviour (pers. obs.).

On 16 December 1978, CBF watched a female perform a most dramatic distraction display by stumbling across the forest floor with fully opened, fluttering wings. He could not see a nest and assumed a fledgling must have been in the immediate area.

Diet

The diet of this species is reported to consist exclusively of insects or arthropods. On 26 September 1979, CBF was in a hide when he heard the frantic loud cries of a tree frog *Litoria* sp. in the middle or upper forest canopy. This was immediately followed by the frog falling to the floor in front of him, pursued by a Bower's Shrike-thrush. The bird chased the frog and took it in its bill, beating it on the forest floor, as they tumbled about. The frog escaped several times but was again chased, caught and beaten until the bird flew up and away with its prey still crying out. The frog had a snout-vent length as long as the bird's skull.

Moult

Birds start moult during November and complete it in March/April. Only one of the 15 birds caught in November had slight wing moult and two had slight body moult. In December seven of the 13 birds were in wing moult, and in January all five captured birds had some wing and body moult. All 11 birds in February and March were in very active body, wing, and tail moult. The single bird caught in April had only a very slight trace of body moult.

DISCUSSION

Our examination of 12 sexed adult specimens and 56 individual mist-netted birds conclusively showed that breeding pairs of Bower's Shrike-thrush are sexually dimorphic. This is contrary to almost all contemporary ornithological literature, which describes or implies that the sexes of this species are alike. The single exception is Galbraith (1974), who correctly suggested from the three sexed adults he examined (one male, two females) the sexual dimorphism we confirm here. He also noted the leg colour to be more purplish and the iris darker in the female. While we observed no sexual difference in leg colour, our photographs of two pairs at their nests suggest that the iris colour of the female is slightly darker and more brown, less red, than that of the male, but the difference is slight.

There remains, however, some confusion concerning the immature plumage of this bird. Officer (1969) described immatures as having rufous-streaks above the lores and above and below the eyes, and with much reduced streaking on the underparts. Simpson and Day (1986) and Morcombe (1986) stated that immatures are browner, duller and more heavily streaked than adults and Reader's Digest (1988) did likewise, adding only that the eye is brown in immatures. Trounson and Trounson (1987) stated only that immatures are browner and duller than adults. Boles (1988) described immatures as being like adults, but having rufous on lores and around the eyelids, with wing feathers edged rufous-olive, and the breast more heavily streaked.

We believe these supposed immature characters with respect to rufous on lores and around eyes in fact refer to the female plumage. The contrary statements regarding streaking on the breast — 'much reduced' (Officer 1969) or 'more

heavily' (Simpson and Day 1986; Morcombe 1986; Boles 1988; Reader's Digest 1988) — misleadingly refer to the possibly slightly heavier grey breast streaking of adult females. The supposed 'browner and duller' immature plumage may refer to the fact that the edges of the remiges are 'warm olivaceous' in the male and 'bright rufous' in the female, as pointed out by Galbraith (1974), and that males are perhaps a slightly darker grey on the upperparts than females.

If immature Bower's Shrike-thrushes, like those of some other *Colluricincla* species, retain the rufous juvenile wing coverts, and if the sexing of the two male skin specimens AM O.45782 and QM O.14940 is correct, then it appears that immature males have a superciliary stripe and grey bill, as do adult females. Plumage changes of an individual captured in October 1981, October 1983 and September 1984 support the conclusion that juvenile males have a rufous eye-stripe which diminishes with post-juvenile moult. This is consistent with plumage changes with age in the Grey Shrike-thrush *C. harmonica* (Disney 1974) in which the rufous superciliary stripe is an exclusively juvenile character that is retained in adult female Bower's Shrike-thrushes. Moreover, Disney's detailed descriptions of plumages and soft part colours of the Grey Shrike-thrush agree with what we describe in Bower's Shrike-thrush as sexual dimorphism in lore and eye-ring feathering colour, slight differences in breast streaking, iris and bill colour.

That the four presumed immature males we netted had black bills, unlike the two immature male museum specimens, may indicate that juvenile males have a female-like grey bill which darkens with age. If this is the case, then at least some of the remaining 25 netted individuals of unconfirmed sex and age (see above) with a superciliary stripe and grey bill may have been young males. This would account for the significantly larger number of birds in adult female than in male plumage.

It is useful to review illustrations of Bower's Shrike-thrushes in the literature, as some confusion has been caused by them, and some clear evidence of sexual dimorphism has been overlooked. The painted figures in Officer (1969), Pizzey (1980), Slater *et al.* (1986) and Morcombe (1986) are adult males. The pen and ink sketch in Blakers *et al.* (1984) is a female. The three painted figures on pages 55 and 73 in Cayley (1987), which contains no text description of plumage, are all females, contrary to the caption on the latter page and on page 783. The Australian Museum specimen numbers from which Cayley painted his plate on page 73 appear on page 783 (male AM O.1650, female O.3423). Our examination of these two skins revealed that they were not in fact sexed by collector or preparator. Cayley correctly painted the lores of his male grey and those of his female rufous, but showed the male with a rufous superciliary stripe that is not present on the unsexed skin he used.

The three fine photographs of Bower's Shrike-thrush reproduced in Boles (1988) are noteworthy, as those on pages 242 and 243 are respectively of a female and a male on the same nest. The bird appearing on page 240 is a female. The photograph in Frith and Frith (1985) is of a female, as is that in Trounson and Trounson (1987).

The results of our netting and banding demonstrate the sedentary nature of Bower's Shrike-thrush, which is clearly a pair-bonding, monogamous and territorial species, as are the better known Little Shrike-thrush *C. megarhyncha* and the Grey Shrike-thrush (Reader's Digest 1988; Boles 1988). The oldest individual we have studied has lived at least eight years, as it was an adult female with well developed brood patch when first caught, seven years before its last recapture. The capture of two apparently mated pairs of birds in March and three in September suggests that the pair-bond lasts beyond the breeding season, as in the Grey Shrike-thrush (Boles 1988).

Our measurements of sexed museum specimens confirm our findings that the sexes are nearly identical in size. This is contrary to the measurements provided by Ford (1979), which indicate a sexual difference in length of wing, tail and, to a lesser extent, tarsus and bill. Unfortunately Ford did not provide the numbers of specimens he examined nor the details of how they were sexed.

The survival rate for Bower's Shrike-thrush of 50 per cent is low (Table 3) for a passerine bird of tropical Australia (Nicholls and Woinarski 1988), and this figure probably reflects the difficulty of capturing and recapturing this species ($\bar{x}$ = 39.5 hours per bird) more than being a realistic assessment of actual survival rate.

The nests we observed and their sites and heights above ground are consistent with previous nesting records. The clutch of three eggs reported here is the first in recent literature of other than two eggs (Beruldsen 1980; Edden and Boles 1986; Boles 1988; Reader's Digest 1988), notwithstanding the bland '2–3' egg clutch size given by Pizzey (1980) and Slater *et al.* (1986), presumably alluding to a clutch of three in the H. L. White egg collection in the Museum of Victoria (B. Gillies, pers. comm.). The sizes of the six eggs we measured ($\bar{x}$ = 28.2 x 20.8 mm) are significantly larger than the approximate 25 x 19 mm given by Beruldsen (1980) and repeated by Reader's Digest (1988), as are those of 23 eggs (10 clutches of two and one of three eggs) in the White collection ($\bar{x}$ = 27.1, SD 1.83, x 19.7, SD 0.58 mm).

The observation of an individual of Bower's Shrike-thrush attacking a medium-sized frog indicates that this bird's diet may be as catholic as is that of the Grey Shrike-thrush in taking a range of small vertebrates in addition to arthropods.

Ford (1979) stated that *C. boweri* is almost midway in wing length between the small-sized *megarhyncha* and large-sized *harmonica* species-groups and concluded that its phylogenetic position was difficult to resolve. On body proportions, he considered *C. boweri* more like the *megarhyncha*-group in almost every respect, and remarked that '*boweri* probably represents an earlier colonizing wave of *megarhyncha* stock from New Guinea'. It is, therefore, noteworthy that the adult sexual dimorphism in *C. boweri* is similar to that in *C. harmonica* rather than the monomorphic *C. megarhyncha*, and that juvenile superciliaries are characteristic of both species (Ford 1979). The colouration and pattern of *C. boweri* eggs are, however, significantly different from the generally very similar eggs of all Australian congeners (Slater *et al.* 1986; Boles 1986).

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