

Breeding biology of the Grey Shrike-thrush (*Colluricincla harmonica*)

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Abstract. Grey Shrike-thrushes (*Colluricincla harmonica*) occur in a wide range of habitats over most of Australia but their life history and breeding behaviour have not been fully documented. Over eight seasons, from 1996 to 2004, we studied the reproductive efforts of Grey Shrike-thrushes using primarily property homesteads as nest sites in the Warrumbungle Mountains near Coonabarabran, New South Wales, Australia. Twenty-four nests were observed at three sites, involving six male and six female birds. Eggs were laid at intervals of ~24 h and the clutch size was usually three (range 2–4). Parents contributed almost equally to incubation, brooding and feeding nestlings and removing faecal sacs during the day, whereas the female alone incubated and brooded at night. After the laying period, the birds combined to incubate the eggs for 93–97% of time. Incubation bouts averaged 41.5 min during laying, 50.7 min during early incubation, and 42.6 min (males) and 50.2 min (females) during late incubation. Mean length of bouts decreased to 10.5 min during the hatchling period and 13.9 min during the early nestling period. The mean incubation period was 17.4 days, the nestling period 15.8 days and the breeding cycle (incubation plus nestling) 32.5 days. Successful fledging of one brood was often followed by re-nesting, with up to three attempts in a single breeding season. The median period to re-nesting (last young fledged to first egg of new clutch) was 16 days, and median length of the breeding season was 18.3 weeks (4.2 months). There was a significant decrease in the length of the nestling period and the breeding cycle for later (second or third) attempts compared with first attempts. Habituated Shrike-thrushes (those nesting near houses; $n = 22$ attempts) fledged on average 2.7 young per nest (89% success rate). Experienced pairs of habituated Shrike-thrushes fledged an average of 3.1 young per nest compared with inexperienced pairs, which averaged 1.3 young per nest.

Introduction

Australia's Pachycephalidae are a group of monogamous, insectivorous birds that range over most terrestrial habitats. Some, such as the Rufous Whistler (*Pachycephala rufiventris*) are broadly distributed, whereas others, such as Bower's Shrike-thrush (*Colluricincla boweri*) have much smaller distributions, owing to range restriction and habitat specialisation. Most species are generally classed as resident or sedentary, with some local movements or altitudinal migration (Blakers *et al.* 1984; Griffioen and Clarke 2002; Higgins and Peter 2002).

Members of the family display a wide range of sexual dichromatism, from sexes being indistinguishable in the field (e.g. Grey Whistler (*P. simplex*), to slightly dichromatic (Olive Whistler (*P. olivacea*), and Crested Shrike-tit (*Falcunculus frontatus*)), moderately dichromatic (Gilbert's Whistler (*P. inornata*)) and strongly dichromatic species (Golden (*P. pectoralis*), Mangrove Golden (*P. melanura*), White-breasted (*P. lanoides*) and Rufous Whistlers). This variation is even more pronounced within the Golden Whistler superspecies in Melanesia (Galbraith 1956; Peterson 1996) with populations on different islands display-

ing all male plumage, all female plumage and a range of intermediate phases.

Although male and female pachycephalids may share nest-building, incubation of eggs, and brooding and feeding of nestlings (Higgins and Peter 2002), the precise roles of the two sexes are generally poorly understood. The only detailed studies of the breeding system of a pachycephalid were carried out on the strongly dichromatic Rufous and Golden Whistlers (Bridges 1994a, 1994b; van Dongen and Yocom 2005). Male Rufous Whistlers incubated eggs for significantly shorter spells than females, whereas male Golden Whistlers performed fewer incubation bouts than females (Bridges 1994a; van Dongen and Yocom 2005). In other strongly dichromatic species, males help in all aspects of the breeding cycle including nest-building, although some Golden Whistler males do not assist with nest-building (Higgins and Peter 2002). Where information is available, Australian pachycephalids are thought to breed in simple pairs, with the exception of the Crested Shrike-tit, where helpers have been seen at some nests (Higgins and Peter 2002) and individuals have been recorded exhibiting extended parental care (Noske 2003).

The Grey Shrike-thrush (*Colluricincla harmonica*) is a sedentary, monogamous bird common in forests, woodlands and scrubs throughout much of Australia. Mean adult weight is 65 g, it shows slight sexual dichromatism and is known to breed in simple pairs (Higgins and Peter 2002) but, despite some early studies (Carter 1924; Gannon 1945), little is known of its breeding biology. The present study was undertaken to determine basic breeding parameters for the Grey Shrike-thrush ('Shrike-thrush' hereafter), especially the contribution of each parent to the breeding effort.

Methods

Study area

Shrike-thrush nests were studied at three sites in the Warrumbungle Mountains (31°17'S, 149°03'E; 800 m asl), ~25 km west of Coonabarabran, New South Wales, Australia, from 1996 to early 2004. In this region, many Shrike-thrushes nest close to houses and sheds, commonly using items such as hanging planters on verandahs. The senior author's house ('the main homestead') is situated in eucalypt forest with trees to within 50 m of the homestead, offering many natural sites for nests. The surrounding forest is dominated by three tree species (*Eucalyptus bridgesiana*, *E. macrorhyncha* and *E. rossii*) with a diverse understorey (including *Acacia caesiella*, *Cassinia quinquefaria*, *Dodonea viscosa* and *Olearia elliptica*). Except for small gaps where homesteads and some light grazing occur, the forest is continuous with the 23 000 ha Warrumbungle National Park.

Observational methods

Shrike-thrush nests were studied during the breeding season (austral spring–summer) by direct observation with the aid of 8 × 30 Swarovski binoculars in the breeding seasons of 1996–97 to 2003–04, supplemented by limited observations in 1995–96. Parental effort during the incubation period was observed for a total of 340.9 h over 63 days, with observation periods averaging 4.3 h (range 0.3–11.7 h). Parental effort during the nestling period was observed for a total of 219.7 h over 56 days, with observation periods averaging 2.5 h (range 0.3–12.4 h). Observations during both incubation and nestling periods were spread as evenly as possible over daylight hours (0530–1830 hours). Observations were also spread as evenly as possible between different nests and between the various stages of incubation and brooding. The building of a new nest was recorded on two occasions for 19.1 and 4.1 h, respectively, with observations spanning daylight hours.

Male and female Shrike-thrushes were distinguished mainly by the plumage of the head and neck and the colour of the bill (Higgins and Peter 2002). In general, the more contrasting colours of the head of males made them easier to see when on the nest, whereas the females' softer streaky grey plumage and paler bill blended more with the surroundings. Pulli were colour-banded from 2002–03, whereas adults were identified by a combination of appearance or behaviour or both (McFarland 1984; Noske 2001). The extent of the white lores and the shade of grey on the crown of males, and the colour of the bill, the extent of streaking and any distinctive markings on the faces of females allowed individuals to be identified. At least as important as these morphological features was the behaviour of the birds, i.e. whether or not they were habituated. Breeding Shrike-thrushes behaved very warily near the nest – a non-habituated bird left the nest every time a person was nearby. Once habituated, birds continued to incubate, brood and even feed nestlings while people were in the vicinity, although they would not approach the nest if a person was nearby.

Behaviour at all stages of nesting was recorded by the senior author, either from inside the house or at least 20 m from the nest if outside.

Birds nesting in the forest were not habituated to people and were extremely wary even if the observer was 30 m from the nest. A hide was needed for observations on one nest in the forest as the adults would not approach if they could see the observer.

The dates and times (all Australian Eastern Standard Time (EST); Daylight Saving Time was converted to EST where necessary) of laying, hatching, fledging and subsequent re-nesting were noted. The time spent by each parent in incubation or brooding bouts and time between incubation, brooding or feeding visits was recorded to the nearest minute. A bout was defined as the time spent incubating or brooding, including time taken to inspect and settle on the nest. Incomplete bouts, when observations began or ended with a bird sitting on the nest, were not included. The time that the nest was unattended was termed the recess period. Feeding visits to nestlings were recorded, with food items identified where possible. The number of faecal sacs removed or swallowed by each parent was also recorded.

Incubation and nestling periods

The incubation period was the time from completion of clutch (laying of last egg) to hatching of the last egg (Marchant 1985). We subdivided the incubation period into three arbitrary periods, with the day of laying of the last egg counted as Day 0: the laying period was Day –1 to the day after the last egg was laid (Day 1); early incubation was the 8-day period between Days 2 and 9; and late incubation was from Day 10 to the time of hatching of the first egg.

The nestling period was the time from hatching of the last egg to when the last young left the nest (Marchant 1985). It was subdivided into a 3-day hatching period (the day the last egg hatched plus the next two days), early nestling (the next 6 days) and late nestling (the end of early nestling to fledging).

Data analysis

Mean values are presented with standard errors (s.e.). Two-tailed *t*-tests were used to detect any significant differences between lengths of bouts of males and females, and incubation or nestling periods for different females. The Pearson chi square statistic was used to test whether males and females differed in their contribution to nest-building (measured as proportion of visits in which they brought nesting material). Pearson correlation coefficients (*r*) were calculated for size or order of clutches or broods against length of incubation, nestling or breeding cycle. Fisher's exact test was used to test whether first clutches were more or less successful than later ones and to compare the breeding success of pairs in different situations (habituated v. non-habituated) and for different clutch-sizes. Finally, median length of breeding season for the pair of birds providing data for five seasons was compared with that of the other three pairs of birds using a Mann–Whitney U test.

Results

Nest-site selection and nest-building

Twenty-four nests, involving six males and six females, were observed in this study. Twenty-two nests were on the outside walls of property homesteads, of which 21 were at five different locations at the main homestead and one was at a nearby property. At the main homestead, habituated Shrike-thrushes nested among foliage or on bare soil in four different planters that were suspended or supported on a plant holder on or near the outside wall of the house. The birds flew under a pergola covered with shade-cloth to reach their nests, which were all situated under eaves at heights of 0.9–1.8 m above the ground and faced south or south-east. The nest site in a planter at a height of 1.6 m at the nearby

property faced west and was partly protected by narrow eaves. The remaining two nests were in eucalypt forest ~400 m from the main homestead and were placed in a dead tree-stump at a height of 1.5 m.

Nests were always well concealed. The male appeared to introduce the female to a nest site by settling his body into a suitable depression in a planter or other support for a nest. The female then inspected the site and, if she accepted it, the pair began building a nest over the next few days. Once a male attempted to persuade a new partner to accept the nest from the previous year by settling into the old nest. The female would not use this nest, but when the male moved to a different, previously unused site and settled into that, the female accepted the site and began nest-building. The five sites used at the main homestead received little or no direct sun. The west-facing site at the nearby property became extremely hot in the afternoon (temperatures as high as 61°C were registered at the nest), resulting in heat stress in the incubating bird (usually the female) and failure of the clutch. The pair of birds at the latter site also exhibited a lack of coordination in change-overs at the nest, and appeared to be inexperienced.

Nest-building occurred in bursts, with the greatest activity between 0600 and 0900 hours and between midday and 1300 hours. Two pairs were observed building. Both males and females brought strips of bark, mainly from Red Stringybark (*Eucalyptus macrorhyncha*), dead eucalypt leaves and fine grasses to form the main structure of the nest. Only females were observed to line the nest, using fine rootlets, after the main structure had been completed. Males brought nest material on 17 of their 35 observed visits to one nest and four of five observed visits at the other. In contrast, females brought nest material on 44 of their 45 observed visits to one nest during building and on each of 11 observed visits at the other nest. Combining the data for the two nests, males brought material to the nest less frequently than females ($\chi^2_1 = 29.6$, $P < 0.001$).

Copulation

Copulation was observed once, at 0605 hours on 4 October 2001, when the nest of the copulating pair was almost completed. The male flew to a perch ~5 m from the nest, calling and fluttering his wings, and the female flew silently to the ground nearby. The female fluttered her wings and tilted her head upwards, making a churring sound. The male flew to the ground 0.5 m from the female. The birds faced one another, both giving an unusual churring call and holding their bodies very stiffly, fluttering the wings and pointing bills upward. After 10 s of this behaviour, the female lowered her head and the male copulated with her for several seconds. They separated, the male resumed the bill-pointing and wing-fluttering, and they copulated a second time ~20 s later, again for only a few seconds. Both birds then flew away. Two eggs were subsequently laid very early in the mornings of 8 and 9 October.

Breeding data

Eight pairs of birds (six habituated, two in the forest), involving six males and six females, nested on one, one, one, one, two, three, four and 11 occasions, respectively, and provided the breeding data used in the present study.

The season usually began in mid- to late August and extended to as late as mid-March. Over eight breeding seasons, duration of the season (first egg laid to last young fledged) for habituated pairs nesting at the homestead ($n = 5$) ranged from 5.3 to 28.6 weeks, with a median length of 18.3 weeks. One pair provided data for five of those seasons, with median length of season of 21.6 weeks (10.0, 18.4, 21.6, 23.6 and 28.6). The median breeding season of the other three pairs was 11.4 weeks (5.3, 11.4 and 18.1). There was no significant difference in length of breeding season for the two groups (Mann–Whitney $U = 2.0$, $P = 0.12$).

For the 24 nesting attempts the mean clutch-size was 2.96 (s.e. 0.11, range 2–4; see Table 1). Clutches were initiated (first egg laid) between August and February (Table 1). Clutches ($n = 8$) laid in August and September were of three eggs; clutches laid in October ($n = 8$) varied in size from two to four; and clutches laid between November and February ($n = 8$) consisted of three or four eggs (Table 1). Although mean clutch-size tended to increase through the season, the difference was not significant ($r = 0.41$, $P = 0.18$).

Over five breeding seasons, pairs that had been together in the previous season ($n = 2$) first laid in August and initiated second clutches in late September or October. Third clutches ($n = 4$) were laid between November and February. Newly formed pairs (i.e. had not nested as a pair in the previous season) first laid in August ($n = 1$) or October ($n = 2$) (Table 1).

Eggs were usually laid early in the morning, once before 0540 hours, but usually between 0630 and 0800 hours. Eggs of a clutch of two or three were laid at intervals of 24–26 h. For the only clutch of four with supporting data, the first three eggs were laid at intervals of roughly 24 h, and the fourth 24–28 h after the third.

Incubation period

The length of incubation was known accurately for seven attempts, with incubation periods ranging from 15 to 20 days, giving a mean duration of 17.4 ± 0.6 days. One female laid four of these clutches, with mean incubation period of 16.5 ± 0.5 days. For this female, second clutches of the season had incubation periods of 15 and 17 days and third clutches, 17 and 17 days (no data for first clutches). For the other two females ($n = 3$ nests), a first clutch of the season had an incubation period of 17 days and two second clutches, 19 and 20 days respectively. None was a replacement clutch.

For nine nests, the approximate time of hatching of each egg was known. All eggs of clutches of two and three hatched on the same day, in daylight hours. The shortest time for three

Table 1. Breeding parameters for eight pairs of Grey Shrike-thrushes with respect to timing of initiation of clutches
Order of clutch in season (i.e. first or subsequent attempt) and experience of pair not known for four clutches

	Month of initiation of clutch							Total (<i>n</i> = 24)
	August (<i>n</i> = 6)	September (<i>n</i> = 2)	October (<i>n</i> = 8)	November (<i>n</i> = 4)	December (<i>n</i> = 1)	January (<i>n</i> = 2)	February (<i>n</i> = 1)	
Clutch-size								
C/2	0	0	4	0	0	0	0	4
C/3	6	2	3	4	0	1	1	17
C/4	0	0	1	0	1	1	0	3
Clutch type								
First clutches	6	0	2	0	0	0	0	8
Second clutches	0	1	4	2	0	0	0	7
Third clutches	0	0	0	1	1	1	1	4
Replacement clutches	0	0	1	0	0	0	0	1
Clutch order unknown	0	1	1	1	0	1	0	4
Pair experience								
Newly formed pairs	1	0	2	0	0	0	0	3
Experienced pairs	5	1	5	3	1	1	1	17
Experience not known	0	1	1	1	0	1	0	4
Nest location								
Close to habitation	6	1	7	4	1	2	1	22
Distant	0	1	1	0	0	0	0	2

eggs to hatch was over a 2-h period, 0800–1000 hours. In a clutch of two, one egg hatched before 0738 hours and the other between 0755 and 0925 hours. The eggs of a clutch of four (*n* = 2) hatched over a period of ~24 h, from before 0725 hours on one day to between 0625 and 0850 hours on the next day.

Males sometimes brought food to a nest containing eggs. This was observed on ten occasions involving three different males at six different nesting attempts. This behaviour was observed on Day -2 (once), Day -1 (once), Day 0 (three times) and Days 1, 2, 3, 9 and 11 (once each). In no case was the female present when the male came to the nest. The male usually settled to incubate with the food in his bill, sometimes eating it soon after settling.

Nestling period

The nestling period ranged from 14 to 18 days (*n* = 12) with a mean period of 15.8 ± 0.4 days. One female laid nine of these broods, with mean nestling period of 15.8 ± 0.5 days. For this female, first broods of the season had nestling periods of 16, 17, 17 and 18 days; second broods, 15 and 16 days; third broods, 14 and 15 days; and for one brood, with period of 14 days, not known if first or subsequent brood. For the other two females, first broods of the season had nestling periods of 16 and 16 days, and a second brood, 15 days. None was a replacement brood.

The longest nestling periods (17 and 18 days) were at colder times of the year (around mid-September), and periods reduced to 14 to 16 days in the warmer months (late September to March). Later (second or third) broods tended to have slightly shorter nestling periods than the first brood (correlation coefficient $r = -0.83$, $0.001 < P < 0.01$).

Time of fledging of 40 chicks from 13 nests is shown in Fig. 1. The chicks of a brood sometimes fledged over a very short period, the quickest being three chicks fledging over 9 min. Most chicks fledged early in the morning, all but four fledging between 0600 and 1100 hours.

Length of cycle

The overall length of one breeding cycle (first egg laid to last young fledged) was determined accurately for 12 attempts and ranged from 32 to 37 days, with a mean of 34.1 ± 0.5 days. One female laid the eggs in eight of these breeding cycles with mean length of cycle of 33.6 ± 0.5 days. For this female, second clutches of the season had cycle lengths of 33, 35, 35 and 35 days, and third clutches, 32, 32, 33 and

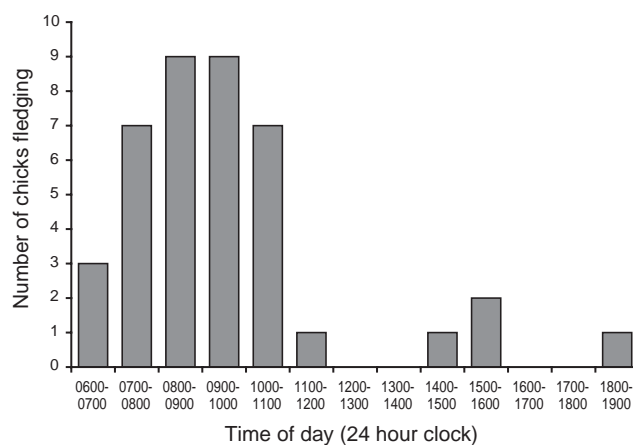


Fig. 1. Time of fledging (Eastern Standard Time) of Grey Shrike-thrush chicks. Data for 40 chicks from 13 attempts; observation time similar for all time periods.

34 days (no first clutches with accurate data). Three other females laid the remaining four clutches, with mean length of cycle of 35.0 ± 0.9 days. For these females, a first clutch of the season had a cycle length of 37 days; second clutches, 34 and 36 days; and for one cycle of 33 days, not known if clutch a first or subsequent attempt.

Larger clutches and later (second or third) clutches tended to have shorter breeding cycles. Although the correlation coefficient r was not significantly different from zero for larger clutches, it was significant for later clutches ($r = -0.18$, $P > 0.10$ for clutch size; $r = -0.78$, $0.001 < P < 0.01$ for clutch order).

Success

Hatching success, measured as the number of eggs hatched ($n = 65$) per egg laid ($n = 71$) was 91.5% (Table 2). Fledging success, the number of young that fledged ($n = 64$) from the number of nestlings ($n = 65$), was 98.5%. Overall reproductive success, measured as the number of fledglings produced per egg laid, was 90.1%, equal to 2.67 young per nest (Table 2). Although the success rate for clutches of three was less than for clutches of two and four, the differences were not significant ($P = 0.34$ for C/2 v. C/3; $P = 0.21$ for C/3 v. C/4; Fisher's exact test). The most successful clutch-size (producing the most young) was four.

First clutches of the season ($n = 8$) were significantly less successful than second, third or replacement clutches (combined data, $n = 12$; $P = 0.015$, Fisher's exact test). More young were fledged from second ($n = 7$) than from first ($n = 8$) clutches (3.00 compared with 2.25 young per nest); and from third ($n = 4$) than from second clutches (3.50 compared with 3.00 young per nest; Table 2).

Clutches of newly formed pairs ($n = 3$) were significantly less successful (57%) than those of experienced pairs ($n = 17$), with a success rate of 98% ($P < 0.001$, Fisher's exact test). Experienced pairs fledged an average of 3.1 young per nest, compared with an average of 1.3 young per nest for inexperienced pairs (Table 2). Previous pairing history was not known in four nesting attempts (two pairs nesting in the forest, one at the nearby property, and the initial habituated pair nesting at the house in January 1996, which nested as an experienced pair in the following year).

Twenty-two attempts were associated with buildings, with overall success of 89% (59 fledglings from 66 eggs). The two attempts in the forest had an overall success of 100% (five from five). The single attempt at the nearby property failed owing to poor nest-site selection, as mentioned above. At the main homestead, one of three nestlings was lost from a nest for reasons unknown, and predation by rats was implicated in the loss of an entire clutch of three eggs. There were no significant differences in success between habituated birds and those nesting in the forest ($P = 0.59$, Fisher's exact test).

Re-nesting

Shrike-thrushes nesting in the forest ($n = 2$) did not re-nest in the same site after being the subject of breeding observations for several days at a time, whereas habituated Shrike-thrushes re-nested in the same site or nearby. Shrike-thrushes were multi-brooded, re-nesting on 11 known occasions after successfully raising at least one fledgling. In three breeding seasons, three pairs re-nested once. One female paired with two different males, re-nested twice in each of four breeding seasons, laying a total of eight, nine, 10 and 11 eggs in those seasons.

Table 2. Reproductive success for eight pairs of Grey Shrike-thrushes in relation to breeding parameters
Data are from 24 breeding attempts. Order of clutch order in season and experience of pair not known for four clutches

	No. of clutches	No. of eggs	No. hatched	% hatched	No. of young fledged	Success (% fledging per egg laid)	Average no. of young per nest
Clutch size							
C/2	4	8	8	100	8	100	2.00
C/3	17	51	45	88	44	86	2.59
C/4	3	12	12	100	12	100	4.00
Clutch type							
First clutches	8	22	19	86	18	82	2.25
Second clutches	7	21	21	100	21	100	3.00
Third clutches	4	14	14	100	14	100	3.50
Replacement clutches	1	3	3	100	3	100	3.00
Clutch order unknown	4	11	8	73	8	73	2.00
Pair experience							
Newly formed pairs	3	7	4	57	4	57	1.33
Experienced pairs	17	53	53	100	52	98	3.06
Experience unknown	4	11	8	73	8	73	2.00
Nest location							
Close to habitation	22	66	60	92	59	89	2.68
Distant	2	5	5	100	5	100	2.50
Overall	24	71	65	91.5	64	90.1	2.67

Table 3. Daytime incubation at various stages of the breeding cycle in the Grey Shrike-thrush

Incubation data from eight attempts with four males and five females in six different pairings. Mean duration of bouts calculated from complete bouts only; mean duration of recess calculated as the time between parental visits to the nest, and this and incubation constancy calculated for sexes combined

Stage of cycle	No. of bouts	Mean bout duration \pm s.e. (range) (min)	% of incubation time	Mean recess duration \pm s.e. (range) (min)	Incubation constancy	Total observation time (h)
Laying						
Male	35	45.7 \pm 4.1 (1–98)	57.5			
Female	32	36.9 \pm 3.8 (5–87)	42.5	18.1 \pm 3.6 (0.5–91)	78.9%	58.7
Early incubation						
Male	87	50.9 \pm 2.8 (4–127)	49.6	5.7 \pm 0.8 (0.3–45)	93.0%	160.1
Female	89	50.6 \pm 3.2 (1–182)	50.4			
Late incubation						
Male	80	42.6 \pm 2.5 (3–100)	48.2	3.2 \pm 0.6 (0.5–22)	96.5%	122.1
Female	73	50.2 \pm 2.7 (2–110)	51.8			

The period to re-nesting was defined as the time taken between fledging of the last young of one attempt and the laying of the first egg of a new clutch in the same breeding season. Accurate data were available for nine re-nesting attempts, with a median interval of 16 days (10, 14, 15, 15, 16, 16, 18, 29 and 49 days). The longest interval, of 49 days, occurred after the fledging of four young (the second brood for the season) and subsequent laying of a third clutch of four eggs in a new nest.

Parental effort during incubation

The female incubated at night. During the day, the male's contribution to incubation tended to peak in early incubation while that of the female increased after laying to a high level maintained through early and late incubation (Table 3; Fig. 2). There were no significant differences in length of incubation bouts between males and females during laying ($t_3 = 0.41$, $P = 0.41$), early incubation ($t_5 = 0.55$, $P = 0.62$) or late incubation ($t_6 = 0.70$, $P = 0.51$). Recess duration decreased through the incubation period, as incubation constancy increased from 79% (laying) to 97% (late incubation).

Parental effort during the nestling period

The female brooded the young every night until the last young fledged, occasionally sitting beside the nest during late brooding period. The nestling period was characterised by rapidly decreasing bout lengths of daytime brooding. The very high incubation constancy during late incubation dropped to 69% during hatchling period and to 19% in the early nestling period (Table 4, Fig. 2). As the nestling period progressed, parents visited to feed nestlings and remove faecal sacs without brooding. Diurnal brooding usually decreased 5 days after the last egg hatched and stopped 6 days after hatching, although occasional brooding occurred at later times, with the latest observation 10 days after the last egg hatched (during heavy rain).

There were no significant differences in length of brooding bouts between males and females during the hatchling

and early nestling periods ($t_3 = 1.81$, $P = 0.21$; and $t_6 = 0.47$, $P = 0.66$ respectively). Brooding bouts were significantly shorter during the hatchling period compared with late incubation ($t_{11} = 4.55$, $P = 0.006$).

Male and female Shrike-thrushes fed nestlings at similar rates (Table 4). For males and females combined, the rate of feeding nestlings was 5.9 ± 0.5 feeds h^{-1} in hatchling period, 4.9 ± 0.3 feeds h^{-1} in early nestling period, and 7.0 ± 0.4 feeds h^{-1} in late nestling period.

A total of 1349 feeding visits was recorded in this study. On a further four visits to nestlings, adults brought no food. On three of these occasions, the adult settled to brood (nestlings aged 0, 2 and 4 days respectively), and once checked the nest after it had been visited by the senior author. Visits by adults to the nest from ~30 min before fledging of the first chick were not included in the feeding data; sometimes they failed to bring food, possibly to entice the young to leave the nest.

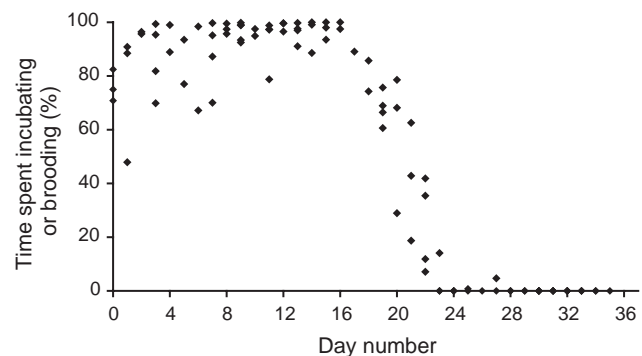


Fig. 2. Incubation and brooding constancy in the Grey Shrike-thrush (data for ten nesting attempts). The figures for incubation and brooding constancy (coverage of eggs or young by both parents as a percentage of observation time) for individual nests are shown as separate points on the graph. Day 0 is the day that the last egg was laid, and Day 17 is taken as the day that the last egg hatched. At the only nest in which incubation of eggs continued past Day 17, the data from Day 18 to hatching are not included in this graph.

Many food items could be broadly identified. Large lepidopteran pupae were favoured items. Other arthropods fed to the young were centipedes, spiders, grasshoppers, dragonflies, beetles, earwigs, stick-insects and insect pupae. Occasionally other invertebrates (earthworms and crustaceans) and small vertebrates (frogs and skinks) were given to nestlings. Large food items such as large insect larvae, frogs and centipedes were occasionally brought to nestlings aged 1–4 days but were generally brought from 5 days of age onwards.

There was a steady increase in the removal of faecal sacs by parents throughout the nestling cycle (Table 4). The rate of removing faecal sacs (male and female data combined) was $1.2 \pm 0.2 \text{ h}^{-1}$ in hatchling period, $1.5 \pm 0.1 \text{ h}^{-1}$ in early nestling period, and $2.5 \pm 0.1 \text{ h}^{-1}$ at late nestling period.

After fledging, juveniles were rarely seen near the nest for more than a few days and their survival was not monitored. It is not known how much care is given to any juveniles once the adults re-nest, but the short period between fledging and re-nesting (~16 days, see above) places a limit on post-fledging care. Immature birds of unknown age have been seen in the parental territory for months following fledging. In late March 2001, one pair were visiting their nest, having reared three broods in the season. When a young bird approached the nest, it was chased away by both adults. Banding of pulli began in 2002–03. One colour-banded bird was seen near the main homestead on several occasions in the months after fledging, and was fed by an adult 70 days after fledging, the last time this young bird was seen.

Mate fidelity and mate replacement

Pairs appeared to be stable. If both partners from the previous year were present at the start of a new breeding season, the same pair of birds often re-used the previous season's nest.

Once, in the 2001–02 season, the female of one pair was killed by a feral cat (*Felis catus*) before the start of the breeding season (late July 2001). By 3 August, the male had attracted a second female which was killed after colliding with a window on 15 September, after renovating a nest but before laying. By the end of September, the male had attracted a third female, and the pair began building a nest on 30 September, fledging two broods in November and December, respectively.

When the male holding the territory at the main homestead left in May 2002, the female deserted the territory and later bred with a male in an adjoining territory. The main homestead territory was taken over by a new female. She paired with a male, built a nest in a hanging planter, but then died a few weeks after fledging two colour-banded young on 28 November 2002.

Once an adult male helped incubate and rear another male's young. The last of three eggs had been laid on 10 February 1997 in a nest in a hanging planter. The resident male was depredated while roosting near the nest on 17 February. The female gave a different type of song while sitting on the nest. A new male appeared and approached the nest cautiously on 24 February (the day before hatching), at which point the female flew off, allowing the male to inspect the nest and then incubate. The new male sometimes sang loudly while incubating. He assumed parental duties, helping to incubate and brood the young. This male and female continued their association over the next four seasons, breeding 11 times and fledging 35 young before the female died in August 2001 and the male disappeared in May 2002. Assuming that adult-plumage birds are in their third year (Higgins and Peter 2002), both birds would have been 7+ years at the time of disappearance or death.

Table 4. Daytime brooding, feeding of nestlings and nest sanitation at various stages of the breeding cycle in the Grey Shrike-thrush
Nestling data from eight attempts of four pairs. Mean duration of bouts calculated from complete bouts only; mean duration of recess calculated as the time between parental visits to the nest, and this and brooding constancy calculated for sexes combined

Stage of cycle	No. of bouts	Mean bout duration \pm s.e. (range) (min)	% of brooding time	Mean no. feeding visits h^{-1} \pm s.e. (range)	Mean no. faecal sacs removed h^{-1} \pm s.e. (range)	Mean recess duration \pm s.e. (range) (min)	Brooding constancy (%)	Total observation time (h)
Hatchling								
Male	58	10.9 ± 1.1 (1–36)	48.9	2.93 ± 0.27 (0–7)	0.67 ± 0.16 (0–2)	5.9 ± 0.7 (0.5–31)	69.0	28.3
Female	65	10.2 ± 1.4 (0.5–81)	51.1	3.00 ± 0.32 (0–7)	0.56 ± 0.15 (0–3)			
Early nestling								
Male	28	12.4 ± 2.1 (1–43)	42.9	2.51 ± 0.19 (0–7)	0.78 ± 0.10 (0–3)	11.2 ± 0.6 (0.5–71)	19.2	70.1
Female	30	15.4 ± 2.3 (1–49)	57.1	2.42 ± 0.20 (0–9)	0.72 ± 0.09 (0–3)			
Late nestling								
Male	1	N/a (17)	–	3.54 ± 0.23 (0–16)	1.24 ± 0.09 (0–4)	9.6 ± 0.4 (0.5–108)	0.2	121.3
Female	0	0	–	3.41 ± 0.22 (0–12)	1.24 ± 0.09 (0–4)			

Habituation

Shrike-thrushes nesting in the forest never became habituated in this study, while Shrike-thrushes nesting at the main homestead for the first time typically took ~5 or 6 days to become accustomed to the presence of people. Habituated birds did not leave the nest if a person remained at least 1.5–2 m from the nest, although they watched the intruder constantly. In contrast, non-habituated birds generally left the nest if people approached within ~5 m. Eye contact scared sitting birds in the early stages of habituation, but later even this was tolerated. However, habituated birds in the process of feeding young were intolerant of people and usually flew away. They scolded anyone who approached fledglings.

Whether habituated or not, Shrike-thrushes did not fly straight to the nest but always approached cautiously and indirectly, appearing to have their own preferred routes using particular perches. They would not approach the nest at any stage of the breeding cycle if people were within ~7 m of the nest.

Calls and song

Five or six different song sequences were sung by males, sometimes with a shorter response by females, at the start and end of the breeding season, possibly to reinforce ownership of the territory. Singing was also common after a period of rain.

During incubation, a typical changeover occurred when the incoming bird gave a Clear Call (Higgins and Peter 2002) when ~20 m from the nest, which was answered sometimes by the bird on the nest. The sitting bird then left, usually 15–30 s before the incoming bird arrived. If the incoming bird did not signal its intention to come to the nest by calling, the sitting bird (especially the male) would give a Clear Call, apparently as a signal to the other parent to take over nest duties. Older nestlings a few days from fledging chirped when food was brought and in response to an adult's call near the nest.

Discussion

A limitation of the present study is that it was carried out largely on habituated Shrike-thrushes with only a small amount of information on birds nesting in natural habitat. The capacity or willingness to nest near people demonstrates that birds can be flexible in their breeding behaviour. However, the nesting situation of habituated shrike-thrushes is not unusual for this species, which has often been recorded nesting in association with people (see, for example, North 1901–1914; Gannon 1945). The Grey Shrike-thrush is the only Australian ptychocephalid recorded as nesting in human-associated sites: 10.8% of 509 nests were in a shed, garage or other outbuilding and 5.5% were under a verandah, porch or carport (Nest Record Scheme, reported in Higgins and Peter

2002). As the study area retains most of its natural vegetation, the birds could presumably choose between natural or human-associated sites for nesting.

This study has clarified the participation of male and female Shrike-thrushes in the overall breeding effort and parental care. In several respects, namely nest-building and nocturnal incubation and brooding, the roles of males and females differed. Although the male helped in building, the female undertook more nest-building than the male and the female did all incubation and brooding at night. In most respects, however, the participation of male and female Shrike-thrushes was comparable, with the sexes sharing equally in the diurnal incubation of eggs, brooding and feeding of nestlings and removal of faecal sacs. This sharing of all nest-based activities may be classed as unspecialised biparentalism (Goodey and Lill 1993).

Detailed data on parental care have been collected for only two other members of the Ptychocephalidae, the Rufous and Golden Whistlers. Incubation bouts of Shrike-thrushes averaged 41.5–50.7 min at different stages of the cycle, considerably longer than those reported for Rufous and Golden Whistlers, where incubation bouts averaged 15.5–21.3 and 18.9–25.4 min (Bridges 1994a; van Dongen and Yocom 2005). The brooding bouts of Shrike-thrushes averaged 10.5–13.9 min at different stages, substantially shorter than those of Rufous Whistlers, which averaged 14.5–22.0 min (Bridges 1994a). Although incubation and brooding bouts were not significantly different between male and female Shrike-thrushes, incubation and brooding bouts were considerably shorter in male Rufous Whistlers compared with females (Bridges 1994a).

Thus, the slightly dichromatic Grey Shrike-thrush shows a more equal division of labour than the strongly dichromatic Rufous Whistler. In species with strong sexual dichromatism, males might be expected to make a smaller contribution to parental care (Trémont and Ford 2000). Brightly coloured males are more likely to seek extra-pair copulations (Møller and Birkhead 1994) and are also likely to be more obvious at the nest. Both Shrike-thrushes and Rufous Whistlers show high levels of biparental care, a condition that favours monogamy (Wittenberger and Tilson 1980). Although the breeding biology of many ptychocephalids is not well known, all species except the Crested Shrike-tit (which may be a cooperative breeder) are thought to be monogamous (Higgins and Peter 2002). This uniformity, coupled with the full range of sexual dichromatism (Galbraith 1956; Peterson 1996), makes the Ptychocephalidae an ideal group to evaluate further the interplay between parental care and dichromatism.

The reproductive parameters measured here are in broad agreement with previous data for the Grey Shrike-thrush. The clutch size measured in this study (mean of 2.96) is close to the mean of 2.89 in NSW (Nest Record Scheme, reported in Higgins and Peter 2002) and 2.97 in NSW and Victoria

(Courtney and Marchant 1971), and is similar to the mean of 2.69 for Australian passerines generally (Yom-Tov 1987). The incubation period (17.4 days) is similar to various estimates of 16.9 days (Nest Record Scheme) and 18 and 19 days reported in Higgins and Peter (2002), and corresponds exactly with the value predicted for a 65 g Australian passerine (Yom-Tov 1987). The length of the nestling period (15.7 days) is similar to that found by others (17–18 days; Gannon 1945; 15.5 days, Nest Record Scheme; Higgins and Peter 2002), but is 5 days shorter than that predicted for a 65-g Australian passerine (Yom-Tov 1987). Nestlings were brooded during the day until they were 5 days old, but with little diurnal brooding from 6 days after hatching, at which time the young are assumed to be capable of temperature regulation. This length of time concurs with the reported brooding period of 6–7 days (nestlings 5–6 days old) (Higgins and Peter 2002).

Anti-predator strategies adopted by Shrike-thrushes include choosing a well-hidden nest-site and approaching the nest at all times via an indirect route. Major (1991) has noted other avian anti-predator strategies, two of which are used by Shrike-thrushes, namely that feathers are not used as nest lining, and that nestlings generally refrain from giving begging calls (at least, up to several days before fledging). Other possible anti-predator strategies are long incubation bouts and a short nestling period. Taken together, these strategies represent a considerable defence against predation, and reinforce the idea that predation has a major influence on a species' breeding biology.

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