CO-OPERATIVE BREEDING BY BLACK-FACED WOODSWALLOWS Artamus cinereus

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From 1973 to 1976, I studied Black-faced Woodswallows *Artamus cinereus* in the wheatbelt of Western Australia, where the species is resident all the year round. By 1975 all the birds in one group were individually colour-banded and their contributions at four nests were recorded during 68 hours of hide-watches. All birds, presumably of both sexes, took part in incubating the eggs, and in brooding and feeding the nestlings.

Despite their widespread distribution and conspicuous behaviour, woodswallows are a very under-studied group. The most thorough descriptions have been those by the late Klaus Immelmann following his incredibly prolific year (1959-60) in Australia (Immelmann 1963, 1966), a briefer account by Clunie (1976), and that of Recher and Schulz (1983). Seasonal movements and geographic variation in the family were summarized by Keast (1958). For the rest, the literature consists of brief snippets of information (Chisholm 1909; Dove 1909; Heathcote 1931; Cameron 1933; D'Ombrain 1934; Coleman 1945; Rowley 1951, 1976b; Hindwood 1956; Immelmann 1960; Sharland 1972; Lowe and Lowe 1972; Bourke 1972; Austin 1972).

Over the past three decades, there has been much interest in co-operative breeding, where more than a single pair help to raise a brood of young. This unusual aspect of biology occurs particularly frequently in old endemic families of the Australian avifauna (Russell 1989). In this regard, the Artamidae, which includes the woodswallows, has been little studied, although it has been included as a co-operative breeder in a number of reviews, from largely anecdotal reports (Rowley 1976a; Dow 1980; Clarke 1995).

Between 1973 and 1976 in the course of other work I was able to catch and colour-band a number of Black-faced Woodswallows *Artamus cinereus* and to follow their behaviour over several years. These data constitute the first quantitative demonstration of co-operative breeding by a woodswallow.

STUDY AREA AND METHODS

Whilst employed by CSIRO to investigate the pest-status of the Galah *Cacatua roseicapilla*, I embarked on a long-term study of a marked population of that species at Manmanning (30°51'S, 117°06'E) in the Western Australian wheatbelt. That study, the area and its climate are described elsewhere (Rowley 1990).

We followed the behaviour of individually wing-tagged Galahs all year round throughout our 95 km² study area. At the same time, we also noted 19 groups of Black-faced Woodswallows (hereafter BFWS) that frequently perched conspicuously on telephone lines in between flying foraging sorties. We also, opportunistically, located their nests, which were usually conspicuous and less than two metres from the ground. In particular, one group of BFWS nested at the north end of the Water Reserve (Conservation Reserve A 25984), an area of 47.6 ha. All nests were chronologically numbered for each year; the seven nests referred to in this paper are given in Bold type, e.g. 7501 was the first nest found in 1975. All seven were exposed, cup-shaped nests built of thin twigs in saplings of *Eucalyptus wandoo*, 1.4-2.0 m above the ground. In this paper, individual birds are referred to by the last three numbers (in italics) of their metal band, which remained constant throughout the study; combinations of colour bands were changed from nestling codes to adult ones as birds matured and to use these colours would confuse readers.

Although most banders will have caught the occasional wood-swallow when mist-netting, to set out to catch a particular bird or group is difficult. We found that setting a mist-net alongside a nest when we were banding young often resulted in catching most of the attendant adults as they swooped in defence of the calling nestlings. By 1975 all members of a group in the north of the Water Reserve were individually identifiable and we started watching nests from a hide nearby to record the birds that attended. All hide-watches lasted longer than 100 minutes and the activity of the birds was measured as follows:-

- (a) Incubation, brooding and shading were timed from when a bird resumed sitting on the nest until the end of the last bout observed.
- (b) *Feeding rate* was calculated as the number of feeds less one divided by the time between the first and last feeds, to give the rate of feeds per hour.

Unfortunately BFWS are monomorphic in plumage and none of the measurements available for them, or for other members of the genus, appear to be reliably diagnostic of sex (Baker *et al.* 1997; B. Dettmann, pers. comm.). Also, because both sexes incubate and develop brood patches, the presence of these bare areas is not diagnostic of sex. Measurements of specimens that had been sexed by dissection, in the collection of the West Australian Museum from the south-west of the state, suggested that males were larger than females (male folded left wing mean 126 mm, range 122–130, n = 7; female, 112 and 114 mm, n = 2). Although this sample size is small, since the wing of 650 measured 128 mm and that of 651, 119 mm, I feel confident that 650 was the male.

RESULTS

When we banded three young (353, 354 and 355) of the Water Reserve group at nest **7301** in November 1973, the four attending adults remained unbanded. In October of the next year, this group raised a Pallid Cuckoo *Cuculus pallidus* and five birds helped to feed it, three of whom were the birds banded as nestlings the previous year. In December, we caught the two unbanded adults (650 and 651) and recaught two of the 1973 nestlings (353 and 355) as they attended nest **7422** where we were banding nestlings 647, 648 and 649. The third 1973 nestling (354) was also seen nearby so that we now had a complete group of individually banded birds. In the following two years we maintained several hide-watches from positions close to four nests of this group.

Throughout the year we resighted colour-banded individuals of this group together, within a home range of approximately 100 ha. This was not an exclusive area, and included other groups of BFWS which were not seen to conflict. The nests reported in this paper were all within five ha, and another banded group also nested within this area, but we saw no aggression between the two groups.

In October 1975, we found **7501** while it was still empty; once the clutch was complete, a hide was placed nearby and gradually moved closer until it was only three metres from the nest and identification of the five attending banded birds was assured. From 5 to 14 November seven hide watches, totalling 22.5 hours, monitored incubation. All five attendants incubated, the putative female and male for 38 per cent and 25 per cent of the time, respectively, one two year old unsexed helper (354) 20 per cent, and the one year old helper (648) 5 per cent; a two year old male helper (355) incubated for 4 per cent of the time, in between attending his own nest where he had been seen to copulate with an unbanded female who sat on two eggs (Table 1a).

It is estimated that the nest hatched on 15 November while we were absent. Between 18 and 27 November nine more watches (32.5 h) followed the brooding, shading and feeding of the nestlings in **7501** (Tables 1b,c and 2). The time spent brooding decreased from 83 per cent when the nestlings were three days old to 53 per cent three days later. By the time the nestlings were ten days old (25November), they were feathered sufficiently to make warming by brooding unnecessary, particularly since temperatures on 25 and 26 November exceeded 38 degrees C. When the nest was exposed to the sun during this very hot spell (60% of the hidewatch), attendants feeding the nestlings usually stayed after delivering food and shaded the open nest with their wings spread (Table 1c).

All five attendants fed the nestlings, the relative proportions varying from day to day. When the nestlings were 3–10 days old and still being brooded, largely by the putative female 651, she fed less than the others. At that time, the yearling helper 648 provided 43 per cent of feeds. Over all watches, the putative male 650, the two year old helper 354 and the yearling 648 each delivered

TABLE 1

Contributions by individual Black-faced Woodswallows to (a) incubation (b) brooding and (c) shading at nest 7501. The nest held three eggs that hatched on 15 November. The breeding pair were 650 and 651 (putative male and female, by measurements).

	Hidewatch			Incubation				Per cent sitting by individuals (bouts)				
No.	Date (1975)	Start (h)	Min	Min (bouts)	%	648'	650² ?M	651² ?F	354³	355 ' M	?	
1	5 Nov	1047	154	120 (10)	78	0	21 (2)	0	22 (2)	19 (2)	38 (4)	
2	6 Nov	1040	203	195 (12)	96	0	35 (4)	41 (5)	10 (1)	4 (1)	9 (1)	
3	7 Nov	0723	183	181 (9)	99	10 (1)	31 (3)	13 (1)	23 (1)	9 (1)	13 (2)	
4	11 Nov	1520	179	151 (7)	84	4 (1)	1 (1)	64 (4)	31 (1)	0	0	
5	12 Nov	0955	233	228 (8)	98	0`´	34 (3)	60 (4)	6 (1)	0	0	
6	13 Nov	1007	199	186 (10)	94	7 (1)	27 (4)	48 (4)	18 (1)	0	0	
7	14 Nov	1000	191	185 (11)	97	17 (2)	17 (2)	29 (4)	37 (3)	0	0	
	5-14 Nov		1 342	1 246 (67)	92	5	25	38	20	4	7	

(b) Brooding

(a) Incubation

	Hidewatch			Brooding				Per cent sitting by individuals (bouts)				
No.	Date (1975)	Start (h)	Min	Min (bouts)	%	64 8 '	650² ?M	651² ?F	354 ³	3554 M	?	
8	18 Nov	1459	220	182 (33)	83	23 (8)	19 (17)	46 (12)	9 (5)	3 (1)	0	
9	19 Nov	0954	157	94 (15)	60	29 (4)	7 (1)	25 (3)	36 (6)	2 (1)	0	
10	20 Nov	0842	251	151 (21)	60	13 (5)	14 (2)	45 (6)	24 (5)	3 (3)	0	
11	21 Nov	0743	240	130 (23)	53	28 (4)	16 (5)	38 (7)	15 (6)	5 (1)	0	
	18-21 Nov		868	557 (102)	64	22	15	40	19	3	0	

(c) Shading

	Hidewatch			Shading				Per cent sitting by individuals (bouts)				
No.	Date (1975)	Start (h)	Min	Min (bouts)	%	648 ¹	650² ?M	651² ?F	354 ³	355* M	?	
12	25 Nov	1436	259	160 (24)	62	28 (6)	27 (7)	28 (6)	17 (5)	0	0	
13	26 Nov	0806	242	145 (19)	60	11 (4)	31 (4)	32 (5)	25 (6)	0	0	

Footnotes to Table 1

¹648: unsexed offspring of 650 and 651 in 1974.

² unaged and unsexed breeding adults caught to 648 in 1974; 650 is putative male.

³354: unsexed offspring from unbanded pair in 1973.

^{4355:} a male sibling of 354, twice seen to copulate with ubF; he was paired at 7518 where an ubF sat on 2 eggs, am 26 Nov. but was empty pm 26 Nov.; on 27 Nov. 355 fed at 7501. In 1976, he again failed with ubF at 7609 on 2 eggs; empty 7 Dec, after which he fed at 7611.

 TABLE 2

 Rate of feeding three Black-faced Woodswallow nestlings, aged 3–12 days, and the proportion contributed by five individuals, at nest 7501. Footnotes as in Table 1.

							Per	cent feed	s made by	/
Date 1975	Age	Start of watch	Mins	Total feeds	Feeds /h	648 [,]	650²	651²	354 ³	355⁴
18 Nov	3	1459	220	39	10.36	36	20	13	31	0
19 Nov	4	0954	157	26	9.55	50	19	8	19	4
20 Nov	5	0842	251	35	8.13	43	11	11	17	18
21 Nov	6	0743	240	36	8.61	42	25	11	19	3
25 Nov	10	1436	259	45	10.18	16	29	29	27	0
26 Nov	11	0806	242	17	3.86	18	18	18	47	0
	11	1646	140	41	17.57	7	44	32	17	0
27 Nov	12	0749	299	89	17.86	24	20	13	24	19
	12	1654	1 07	45	25.23	18	20	7	11	44
18-27 No	v		1 915	373	11.69	27	23	16	22	12

TABLE 3

Rate of feeding four nestlings, estimated seven days old on 13 December, fed by four attendants at Black-faced Woodswallow nest 7611*. Footnotes as in Table 1.

Date 1976		Start watch		Total feeds	Feeds /h	F	Per cent feeds made by					
	Day		Mins			648 ¹	650²	651²	3554			
13 Dec	7	1625	137	19	7.88	26	37	26	11			
15 Dec	9	1021	154	24	8.96	0	37	54	8			
21 Dec	15	0732	175	36	1 2.34	0	44	19	36			
13-21 Dec			466	79	10.27	6	40	32	22			

*354 that helped at nest 7501 the previous year was paired and nesting 200 m to the south.

approximately one quarter of the feeds. Male 355 was obviously distracted by his own nest **7518** until it failed, after which he helped intensively at **7501**. The morning of 26 November was particularly hot and the feeding rate over four hours was less than four feeds per hour compared to the more normal 10 feeds per hour previously. Once a cool change arrived (pm 26 November) the feeding rate rose rapidly and on the final day when the nestlings were 12 days old reached a peak of 25 feeds per hour. On 28 November, three nestlings were banded (665, 666 and 667), all of which fledged successfully (Tables 1c and 2).

In 1976, on 22 September we found **7601** being built, and on 30 September 355 was seen to copulate there with an unbanded female; that nest failed by 14 October. Nearby and contemporary, **7602** was watched for 4.5 h on 14 October, the day before the three eggs hatched and four birds, 648, 650, 651 and 666 incubated. After a very strong gale, the nest had tipped and the nestlings were dead on the ground below on 20 October. Yearling 666 was not seen again. Male 355 and his mate later renested at **7609**.

On 10 December, 7611 was found with four seven day old nestlings attended by 648, 650, 651, and 355. We mounted three hidewatches (8.5 h). From these few watches it would appear that 648 disappeared after 13 December (presumed killed) and the female raised her feeding rate to 54 per cent of feeds. Although male 355was also attending an unbanded female on two eggs at 7609, he was seen to feed at 7611 twice during both 13 and 15 December hidewatches. By the time of the third watch (21 December) **7609** had failed, and 355 fed 13 times at **7611** and female 651 reverted to a lower rate (Table 3).

In 1976, 354 who had helped at **7501** nested separately with an unbanded mate 200 m south of the main group with which it was not seen to interact that year. The study was not continued further, since our Galah project at Manmanning was completed.

DISCUSSION

Woodswallows are aerial foragers, hawking for insects above the vegetation and therefore they are not utilizing a fixed resource that needs to be defended against competitors by maintaining an all-purpose territory, as happens with most resident terrestrial insectivores. Outside of the breeding season several groups of BFWS may forage together and all the year round there is a strong tendency for groups to merge, clustering to roost at night (IR, unpubl. data). In many ways the ecology of woodswallows parallels that of bee-eaters that also breed co-operatively; however, the latter tunnel nests into the ground and tend to nest colonially wherever the soil is suitable. Both groups are very sociable, tending to flock when not nesting, and so it is not surprising that prolonged parental care should lead to helping at parental nests in successive years. The return of male 353 to feed at the family nest after the failure of his own nest is similar to behaviour reported by

Emlen (1990) for White-fronted Bee-eaters Merops bullockoides.

At Manmanning much of the landscape had been cleared for wheat farming so that suitable nesting sites were generally spaced well apart and there was little opportunity for intraspecific competition. Where plenty of vegetation remained, the nests of neighbouring groups were seldom closer than 100 m and intraspecific aggression was rarely seen; occasionally groups combined to repel a predator. BFWS build a cup-shaped shallow nest that is usually conspicuously placed at a site where access is easy for fast flying attendant birds — an open shrub, telephone pole or even the hollow top of a fence post. Inevitably such sites are vulnerable to predation and the value of several pairs of eyes keeping watch is an obvious advantage of cooperative breeding. The area within 5 m of the nest was defended against any intruder, whether a potential predator, a foraging insectivore, or an inquistive ornithologist, but this hardly deserves to be called territorial defence.

The results presented in this paper clearly show that all members of a group of BFWS attending a nest took part in incubating the eggs and brooding, shading and feeding the nestlings. The presumed female 651 took the major share of incubation and brooding, but did not feed as much as the main helpers; all members of the group participated in the defence of the nest. I do not have details of nest construction by this group, but from other groups at Manmanning we know that several birds take part. Although I cannot ascribe sex with certainty to any individual other than male 355 (who was seen to copulate twice), I am reasonably confident that 650 and 651 were the basic pair and active as such in at least 1974, 1975 and 1976, and possibly in 1973. The known-age attendants, 354, 355, 648 and 666 show that progeny may stay with their natal group for up to three years and, presumably, are helping to feed their younger siblings.

I have no data about extra-pair matings as such things were not even considered then! From these limited observations, known age individuals bred for the first time at two years (355) and three years (354). Neither of these birds dispersed very far, which, in the case of 355, appeared to pose some problems of allegiance. This study showed that in a resident population of BFWS, young birds may stay in their family home range for several years. Because of the aerial feeding habit, there is no need for them to disperse and helping in this population of BFWS may be regarded as a form of extended parental care that ensures the survival of progeny until they are experienced enough to breed on their own. The origin of helpers in more nomadic populations of this or other species of *Artamus* will be much more difficult to determine.

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