BREEDING OF RAINBOW BEE-EATERS IN SOUTHERN VICTORIA

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Rainbow Bee-eaters *Merops ornatus* studied over a six-year period in southern Victoria excavated nesting burrows in creek banks and nearby flat or sloping terrain; sites, but not burrows, were commonly used in more than one season. Nesting dispersion varied from solitary to loosely clustered. Egg-laying commenced in early November and hatching and fledging peaked in December and January, respectively. Mean clutch size was 4.5 and the incubation and nestling periods averaged 25 and 28 days, respectively. Mean egg success was 40 per cent. Nesting mortality was mainly due to hatching failure, heavy precipitation and disease or malnutrition; only 12 per cent was caused by predators, mainly the exotic Red Fox. The results are compared with the limited breeding data available for other locations and bee-eater species.

INTRODUCTION

The burrow-nesting bee-eaters (Meropidae) have a predominantly tropical, Afro-Asian distribution; the few species that do breed in the temperate zone overwinter in the tropics (Fry 1984). The Rainbow Bee-eater, the only Australian representative of the family, breeds throughout most of mainland Australia in open or lightly wooded country which provides suitable sites for excavating its nest burrows. It is present throughout the year in tropical northern Australia, but a regular breeding migrant in southern temperate regions (Pizzey 1980).

Although the species is common and conspicuous, its breeding biology is poorly documented. Species such as this, which breed over such a broad geographic range, are especially useful in evaluating the significance of latitudinal and regional variation in reproductive parameters. Such variation is of interest not only amongst bee-eaters, but also in the Australian avifauna generally, where some intriguing trends occur e.g. in clutch size (Yom-Tov 1987).

Hole-nesting species are generally less susceptible to nest predation and have slower growth rates than other altricial land birds (Lack 1968; Ricklefs 1969). While such reduced growth rates may be adaptive in several ways, the nature of any causal link between the two traits remains controversial (Ricklefs 1983). Bee-eaters have slow growth rates (Fry 1984), but there are few estimates available of the contribution of predation to nesting mortality in this family.

While studying the reproductive ecophysiology of Rainbow Bee-eaters in southern Victoria, I systematically recorded nest site characteristics, the timing of breeding, clutch size, reproductive success and nesting mortality factors. The aims were to document the basic breeding biology of a southern population, to gauge the role of predation in nesting mortality and to gather data helpful in evaluating variation in reproductive parameters among bee-eaters and Australian land birds.

METHODS

The investigation was conducted near Lara, 55 km SW of Melbourne from 1986–1992. Migratory Rainbow Bee-eaters arrived to breed in October and departed in March. The study population

bred along a 12 km stretch of Hovell's Creek which follows the ecotone between highly disturbed, dry, open eucalyptus forest and arable farmland and then runs through open paddocks with scattered eucalypts. In summer the creek flows only after very heavy rainfall. During the breeding season, mean monthly rainfall is 46 mm and mean daily maximal and minimal temperatures are 24.2°C and 12.4°C, respectively.

Only a few birds in the population were banded during the study, but some individuals could be identified throughout a particular breeding season by natural or induced plumage variation (e.g. tail streamer size and shape). Nest contents were examined with a 4.8 v light source mounted on a flexible cable and a small, hinged mirror attached to a long, metal rod. Nests were monitored regularly from late October until the end of fledging and inspection frequency was increased to daily or every few days when critical events were anticipated. Access to some nests for physiological measurements (Lill and Fell, unpubl. data) was gained by excavating a hole in the rear wall of the chamber, blocking it with 1 mm mesh flywire and repacking the access shaft with the excavated soil.

The several breeding parameters monitored were measured variously over 3–6 seasons, depending on the time demands of other aspects of the study. The most complete data were collected in the four seasons from 1988–1991, when I attempted to find and monitor all nests in the study area. Because sample sizes for some parameters in some seasons were modest, statistical testing of annual variation is inappropriate. Clutch size determinations were categorized according to whether nest monitoring began before, during or after the completion of laying. Similarly, estimates of reproductive success were differentiated according to whether monitoring began pre- or post-laying. Eggs and/or nestlings were collected under permit from some nests; estimates of reproductive success for these breeding attempts were based on the reduced clutch or brood size and this variable ('manipulation') was taken into account in the analysis.

Data in the nest record scheme (NRS) of the Royal Australasian Ornithologists Union were also analysed with respect to timing of breeding and reproductive success; most of these records were for temperate regions of Australia.

RESULTS

Nest sites

From 1988–1991 when the breeding population was monitored fully, 65 per cent of the 106 nesting burrows in which breeding was attempted were excavated in the creek banks or shoulders (seasonal range 58–78%), 30 per cent on sloping or level ground near, but not on the watercourse (range 20–37%) and 4 per cent (range 0–10%) in the banks of tributary gullies of the main creek. This overall order of preference was also observed in each study season.

From nest spacing and the spatial dispersion of breeders, 62 distinct nesting sites (e.g. a distinct 20 m stretch of creek bank or a particular tributary gully) were identified during the study. For 30 of these sites that were monitored variously for two to six seasons, the average occupancy rates (i.e. the mean ± SD proportion of seasons in which they were used for nesting) were: 0.75 (2 sites monitored for 2 seasons), 0.59 ± 0.22 (9 sites monitored for 3 seasons), 0.56 ± 0.26 (8 sites monitored for 4 seasons), 0.52 ± 0.41 (7 sites monitored for 5 seasons) and 0.39 ± 0.25 (4 sites monitored for 6 seasons). Thus site re-use was quite common.

Those sites that were used more than once were often occupied in two consecutive seasons (56% of 39 possible sites), but longer periods of consecutive occupancy were much rarer (29% of 21 possible sites). Nonetheless, nearly a quarter of the sites that were occupied in more than one season and monitored for the entire six seasons of the investigation were used for five or six consecutive seasons. However, burrow re-use was rare. Only three (2.8%) of 109 monitored nesting attempts in the 1988–1991 period were in previously used burrows; two involved burrows used in the previous season, possibly by the same breeding units, and one involved within-season re-use of a burrow definitely by the same breeding pair which could be recognized by plumage characteristics.

Minimal and maximal distances observed between two simultaneously active burrows were 10–15 m and 200–250 m, respectively. Dispersion of nesting burrows within seasons ranged from solitary to locally loosely clustered. The most pronounced clustering observed involved four simultaneously active burrows all within 20–40 m of one another.

Timing of breeding

The earliest date on which egg-laying commenced was 1–3 November and the latest for any nest was 8–13 January; however, 79 per cent of clutches were initiated between 1 November and 5 December (Table 1). The few clutches started in late December and early January were laid either at sites where breeding was habitually late or by individually recognizable birds re-nesting after failure. However, the latter phenomenon was rare, only five probable instances (4.6% of recorded breeding attempts) being observed between 1988 and 1991.

Hatching was recorded from late November to mid-February, but 81–83 per cent of clutches began hatching between 6 and 26 December. Similarly, although fledging was recorded from 7–8 January to 28 February–1 March, 80–82 per cent of broods began fledging between 3 and 23 January.

Thus, despite the considerable overlap in the timing of these major reproductive events, breeding was sufficiently synchronized for there to be distinct, non-overlapping peaks in egg-laying, hatching and fledging.

Clutch size

Mean size of 119 clutches laid over six breeding seasons (1986–1991) was 4.5 ± 0.9 (range 2–8, mode 4). The three types of clutch size determination (see Methods) yielded very similar frequency distributions. When all determinations were combined, the clutch size frequency distributions for the four consecutive seasons of most intensive monitoring were similar, with clutches of four and five eggs comprising 85–88 per cent of those laid in any season (Table 2). The timing of laying indicated that a few of the larger clutches (six and eight eggs) probably involved some intra-specific brood parasitism (cf. Emlen and Wrege 1986).

Duration of breeding events

Laying intervals (the number of days between the laying of successive eggs in a clutch) and hence laying periods (the number of days taken to complete a clutch) for clutches of any given size varied greatly. Eggs were laid daily in some clutches, but more commonly laying intervals between some or all eggs in a clutch were more than one day. Thus for the two most common

TABLE 1

Timing of bee-eater breeding events over five consecutive seasons at Lara.

Date	Percentage of breeding events initiated					
	Egg laying		Hatching		Fledging	
1–7 Nov.	7.4					
		6.2				
8–14 Nov.	23.5					
		12.4				
15–21 Nov.	19.8					
		7.4				
22–28 Nov.	8.6					
		1.2				
29 Nov.–5 Dec.	4.9		3.8			
6–12 Dec.			17.5			
		1.2		2.5		
13–19 Dec.			32.5			
		1.2		7.5		
20–26 Dec.			15.0			
		1.2		1.3		
27 Dec.–2 Jan.	2.5		5.0			
		1.2		1.3		
3–9 Jan.	1.2		3.8		12.8	
						2.6
10–16 Jan.			1.3		35.9	
				2.5		2.6
17–23 Jan.			2.5		25.6	
				1.3		2.6
24–30 Jan.			2.5		5.1	
31 Jan.–6 Feb.					5.1	
14–20 Feb.					5.1	
28 Feb.–6 Mar.					2.6	
N (breeding attempts) =	81		80		39	

For each breeding phase, the left-hand column gives percentages of events whose initiation could be ascribed to one-week periods and the right-hand column percentages of those which could only be ascribed to two-week periods. The two columns together total 100 per cent.

TABLE 2

Distribution of bee-eater clutch sizes at Lara over four breeding seasons. Distributions given as percentages of observations for a given season.

Season	Clutch size						No. of obs.
	2	3	4	5	6	8	
1988–89	0	7.7	61.5	23.1	7.7	0	13
1989–90	5.9	5.9	41.2	47.1	0	0	17
1990–91	4.0	0	52.0	36.0	8.0	0	25
1991–92	0	8.1	43.2	43.2	2.7	2.7	37
All	1.8	4.6	40.0	32.7	3.6	0.9	110

clutch sizes of four and five (n = 52), 83 and 91 per cent, respectively, of laying periods exceeded clutch size minimally by one to five days. Some of the few very long laying intervals recorded (e.g. eight to nine days) probably involved laying by multiple females.

Incubation periods (from the completion of laying to the completion of hatching) and nestling periods (from the completion of hatching to the completion of fledging) were determined to within three or fewer days. The shortest and longest incubation periods observed were 23–24 and 28–30 days, respectively, and the mean duration was 25 days (n = 15 clutches of various sizes in four seasons). The shortest and longest nestling periods recorded were 23–25 and 33–35 days, respectively, and the mean duration was 28 days (n = 27 broods of various sizes in three seasons).

Hatching and fledging synchrony were not monitored very precisely. However, in a sample of 30 broods containing two to six nestlings, some (maximally 83%) definitely exhibited synchronous (i.e. same day) hatching, but at least 16 per cent hatched asynchronously, taking minimally two to three days and in some cases possibly longer. In a partly overlapping sample of 27 broods in which two to four nestlings fledged, some (maximally 85%) definitely fledged synchronously (same day), but at least 15 per cent fledged asynchronously, taking minimally two, four or five days.

Reproductive success

Hatching success (percentage of eggs that hatched) was systematically monitored for five seasons (1987–1991). Unmanipulated clutches in nests found pre-laying (see Methods) had a mean hatching success of 68.4 per cent (range 0–100%, n = 53). When all manipulated clutches and those found post-laying were included, mean hatching success was virtually identical at 68.2 per cent (range 0–100%, n = 91). Seasonal mean values ranged from 40 to 83% (n = 10–31 clutches). Percentage hatching success for the two most common clutch sizes of four and five eggs did not differ significantly (z = 0.10, P>.05, n_1 = 20, n_2 = 40, Wilcoxon-Mann Whitney test). At least one egg hatched in 79.8 per cent of the 109 clutches monitored sufficiently well to assess hatching success at this level.

Egg success (percentage of eggs laid which gave rise to fledglings) was monitored fully in three seasons (1988–1990). Mean egg success for unmanipulated clutches laid in nests found pre-laying was 39.3 per cent (n = 29). When manipulated clutches and those found after laying were included, the mean value was essentially identical (39.8%, range 0–100%, n = 55). Seasonal mean values ranged from 39 to 43 per cent (n = 11–26 clutches). At least one bee-eater fledged in 61.5 per cent of the 65 breeding attempts monitored fully enough to determine reproductive success at this level.

At these success rates, mean fledging success (the percentage of hatchlings which fledged) can be calculated to be 58.1 per cent and the average clutch of 4.5 eggs would yield a mean of 3.1 hatchlings and 1.8 fledglings.

Nesting mortality factors

The principal causes of embryonic mortality were hatching failure, heavy precipitation and desertion (Table 3). The first category comprised eggs that survived intact to hatching time in active nests, but failed to hatch; a few were known to be infertile or to contain embryos whose growth was defective, and the rest were assumed to be similar. Flash flooding of Hovell's Creek occurred once in each of the 1987–88 and 1988–89 seasons, destroying a total of eight nests and their entire clutches. Predation accounted for less than 5 per cent of embryonic mortality; the predators involved could not be identified, but no structural damage to the nest was involved. The cause of egg breakage was unclear, but it was probably effected by the birds themselves in those instances where eggs were discarded from the nest (Fry 1972b). Forty-three per cent of the clutches depleted by mortality failed entirely, mainly through desertion and flooding.

Forty-four per cent of nestling mortality could not be ascribed with complete certainty to a known agent; the nestlings simply disappeared (Table 3). However, these losses were probably mostly due to either disease or malnutrition, as the other identified mortality factors could effectively be eliminated. For example, in 1991–92, two periods of 2+ days of continuous, heavy rain were followed by heavy nestling mortality within a week. It was uncertain whether some pathogenic effect of rainwater

TABLE 3

Causes of bee-eater nesting mortality at Lara.

Mortality factor	Percentage contribution to mortality		Percentage of depleted breeding attempts affected[5]	
	Embryonic (n=106)	Nestling (n=91)	Clutches (n=44)	Broods (n=36)
Hatching failure	41.5		72.7	
Flooding/heavy rain[1]	26.4	26.4	22.7	16.7
Desertion	18.9	0.0	13.6	0
Predation[2]	4.7	19.8	2.3	25.0
Egg breakage	4.7		6.8	
Disease/ malnutrition[3]		7.7		13.9
Nest destruction by livestock	0.0	2.2	0.0	2.8
Unknown[4]	3.8	44.0	9.1	58.3

Embryonic and nestling mortality measured over five and three seasons respectively.

[1]Includes destruction of nest contents and effects of seepage or food supply reduction.

[2]Includes eggs abandoned after disturbance by predators.

[3]Often impossible to distinguish these two factors

[4]Eggs or nestlings disappeared due to unidentified agency; predation, precipitation and nest destruction not involved.

[5]Some attempts depleted by more than one factor.

seepage down to burrow levels in the nesting banks or malnutrition stemming from poor feeding conditions during the precipitation was ultimately responsible for the deaths, although the latter seems more likely (cf. Fry 1984). Thus up to 52 per cent of nestling mortality could have been attributable to disease and/or malnutrition.

Predation accounted for a greater proportion of nestling than of embryonic mortality ($\chi^2_{(1)}$ = 12.284, P<.001). Only 22.2 per cent of predation on nestlings appeared to be attributable to indigenous predators; Common Brown Snakes *Pseudonaja textilis* were suspected, because they were observed several times near or in burrows without contents. Only one case of nest predation, apparently by a native predator, involved the killing of a breeding adult as well as nestlings. 77.8 per cent of nestling mortality caused by predation was attributable to the exotic Red Fox, *Vulpes vulpes*, which dug out the nest from

behind or in front of the chamber towards the end of nestling development and consumed the entire brood.

Considering embryonic and nestling mortality combined, predation accounted for only about 12 per cent of all losses and foxes were responsible for 61 per cent of these. Flooding and heavy rainfall caused 26.4 per cent of mortality and were involved in the reduction of 16 of the 80 broods and clutches depleted by mortality.

DISCUSSION

The solitary to loosely colonial nesting dispersion of Rainbow Bee-eaters at Lara is probably common in the species throughout Australia. Fry (1984) described a population in Perth, Western Australia, comprising 34 breeding units, mostly well separated, but with some nests only 50 m apart and an absolute minimum inter-nest distance of 2.5 m. Most other bee-eaters in the genus *Merops* nest in dense colonies (Fry 1984), but this has only occasionally been noted in Rainbow Bee-eaters (Peckover and Filewood 1976; Salter 1988). Whether the generally less clumped nest dispersion of Rainbow Bee-eaters reflects a greater availability of suitable nest sites or a different cost:benefit ratio associated with coloniality is unknown.

Bee-eaters range from obligate cliff-nesters to species which always construct their burrows in flat ground (Fry 1972a). Rainbow Bee-eaters choose nest sites opportunistically, variously constructing their burrows in flat or sloping ground, gravel heaps, vehicle ruts, ridges, creek banks and low cliffs. Thus the Lara population mainly used banks, with only 30 per cent of nests being dug in flat or sloping ground, but 93 per cent of a population in Perth nested in the latter kind of situation (Fry 1984). Extensive re-use of the same localized breeding site for two to three (or more) years as observed at Lara is not typical of all bee-eaters; Emlen (1990) and Fry (1972b) report annual nest site switching rates of 81 per cent and 97 per cent in truly colonial White-fronted Bee-eaters *Merops bullockoides* and Red-throated Bee-eaters *M. bulocki*, respectively. However, re-use of the previous year's burrow was rare at

Lara and is apparently relatively so in other Rainbow Bee-eater populations and bee-eater species (Morris 1977; Fry 1984; Emlen 1990). This may be advantageous at least partly in avoiding the ectoparasites and pathogens which accumulate in the uncleaned nest chamber during breeding.

The onset of breeding primarily in November–December at Lara accords with other records for south-east and south-west Australia (Morris 1976 and 1977; Courtney 1971; Beruldsen 1980; Fry 1984). Further north, suitable conditions clearly occur earlier, breeding commences in August–September and the season may extend until April (Carruthers 1975). Most nestlings at Lara fledged in January; because this is only one to two months before the autumn northward migration and the period of fledgling dependence is substantial (Fry 1984), it is hardly surprising that re-nesting after failure was so rare at this location. Seventy-six per cent of the 19 broods in the NRS for which fairly accurate dates could be calculated also fledged in January.

Mean clutch size among bee-eater species ranges from 2.9 to 4.9, with a marked latitudinal gradient from one to two eggs near the equator to 6–10 in the temperate zone (Fry 1984). The mean clutch size recorded at Lara is similar to estimates for Rainbow Bee-eaters at other locations derived from much smaller samples. Although it accords well with the latitudinal clutch size gradient recorded for the family, there is little suggestion of such a gradient within this species, which breeds from about 9 to 38°S, although reliable records, especially for the tropics, are sparse. Some other widespread avian taxa in Australia similarly lack such a gradient (Yom-Tov 1987).

Bee-eaters have long incubation periods *(I)*, ranging from about 19 to about 25 days (Fry 1972a). Mean *I* of Rainbow Bee-eaters at Lara, 25 days, was 1.5–1.6 times greater than the value predicted allometrically from adult body and egg mass (Rahn and Ar 1974; Lill, unpubl. data), but there are too few estimates for other bee-eater species to assess whether this relationship is typical of the family. The nestling period *(N)* was also protracted, being, on average, only two days shorter than the highest mean duration recorded among bee-eaters, which is 30 days in the much heavier Carmine *Merops rubicus* and European

M. apiaster bee-eaters (Fry 1984; Ar and Poinkewitz 1992). Mean duration of the various stages of breeding recorded at Lara matched more narrowly based estimates for Rainbow bee-eaters at other Australian localities (Fry 1984).

N varied by the surprisingly large factor of 1.5 among Rainbow Bee-eaters at Lara. Lability of developmental rate is not a general characteristic of bee-eaters, but Emlen *et al.* (1991) reported a nearly twofold variation in *N* in the White-fronted Bee-eater; they argued that it reflected the ability of nestlings to survive food shortages by temporarily reducing their metabolic rate. The longest nestling periods recorded at Lara were not obviously associated with any general seasonal food shortage in the area, judging by the duration of contemporaneous breeding attempts. However, they could have resulted from localized food shortages experienced by particular breeding units.

The degree of hatching synchrony varies strikingly among bee-eater species. In some, markedly asynchronous hatching leads to significant intra-brood mass disparities and differential mortality when food resources are limited (Bryant and Tatner 1990; Emlen *et al.* 1991). Marked and persistent mass disparities of this kind occurred in some Rainbow Bee-eater broods at Lara, but hatching synchrony and nestling growth were not monitored comprehensively enough to determine whether mortality induced by starvation particularly affected late-hatching, underweight nestlings.

Predation was a relatively minor mortality factor and attributable mainly to an exotic species which cannot have had a major influence on the evolution of the bird's reproductive biology. The main indigenous nest predators on Rainbow and other bee-eaters are snakes, lizards, small mammals and even raptors (Fry 1972a, 1984). Predation also accounted for less than 3 per cent of clutch and 5 per cent of nestling losses in the White-fronted Bee-eater (Emlen 1990) and was an insignificant nesting mortality factor in Blue-throated Bee-eaters *Merops viridis* (Bryant and Tatner 1990). Thus burrow-nesting does seem to confer considerable protection against nest predation in bee-eaters. While this must make slow development less costly, its effect may be

partly counteracted by the obvious susceptibility to heavy precipitation experienced by nesting Rainbow and some other bee-eaters (Fry 1984).

There are few reliable data on breeding success and nesting mortality factors for other Rainbow Bee-eater populations or bee-eater species. Australia-wide, 69 per cent of Rainbow Bee-eater breeding attempts result in some success and, on average, 1.7 fledglings are produced per attempt (NRS, n = 55), figures very similar to those obtained in the present study. Compared with present estimates for the Rainbow Bee-eater, hatching success was fairly similar in tropical White-fronted (75%) and Blue-throated (59%) Bee-eaters, but fledging success was 20% lower in the White-fronted Bee-eater (Emlen 1990; Bryant and Hails 1983). Egg success was much higher (78–95%) in the Red-throated Bee-eater (Fry 1972a), but much lower in the White-fronted Bee-eater (26%) (Emlen 1990). In the latter species, starvation was a major cause of nestling losses (35%), as it probably was in the Rainbow Bee-eater.

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