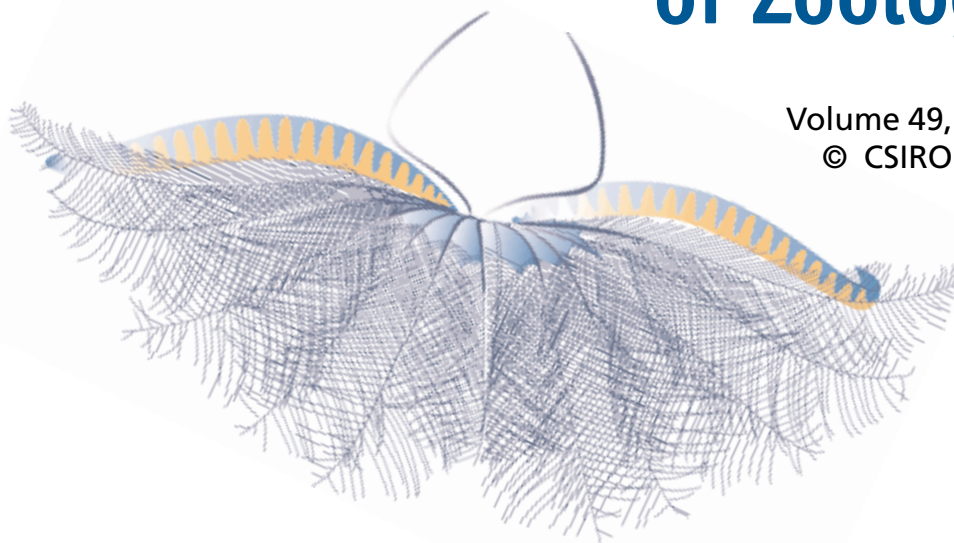


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**Kingfishers in paradise:  
the breeding biology of *Tanysiptera sylvia*  
at the Iron Range National Park, Cape York**

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*Abstract*

We describe the breeding biology and site fidelity of the buff-breasted paradise kingfisher (*Tanysiptera sylvia*), which migrates each year from New Guinea to breed in north-east Australia. In a three-year study at the Iron Range National Park in Cape York, Australia, we collected data from 91 breeding attempts (49 territories), and banded 77 adults and 101 nestlings (47 broods) to determine site fidelity. Paradise kingfishers arrived at Iron Range when the first major rains fell after the dry season. They nested exclusively in terrestrial termitaria, avoiding mounds that were too small, too close to a neighbouring territory, or mounds where the termites were absent. They were single-brooded, but laid a second clutch if their first attempt failed early. Clutch size was usually three, incubation lasted 25 days, nestlings hatched asynchronously and fledged after 27 days. Of 114 nestlings, 48.2% were male. Each breeding territory produced an average of 1.5 fledglings per year. The main factors influencing nesting success were predation, which ended 33% of all attempts, and brood reduction, which affected 24% of nests. Hatch failure was rare (3.2%). Birds were sexually mature at one year. Nearly half of the breeding adults banded in the first year of the study were still alive two years later, making them at least four years old. The return rates of banded adults varied among years (56–84%), but were similar for the two sexes. Returning birds almost always settled on the same territory with the same partner as the previous year, thus they formed long-term pair-bonds. In all, 7% of breeding pairs were assisted at the nest by an additional male, who was probably not their offspring.

**Introduction**

Buff-breasted paradise kingfishers (*Tanysiptera sylvia*) are one of the many avian species that migrate each year across the Torres Strait from New Guinea (Draffan *et al.* 1983) to breed in the rainforests of north-east Queensland. The arrival in Australia of these spectacular birds is noted by many, yet information on their breeding biology and migratory patterns is scarce. For example, an important breeding population was discovered in the Mackay region as recently as the early 1980s (Nix 1984; Brickhill 1986; Andrews *et al.* 1991).

Paradise kingfishers are known to breed in five areas of lowland rainforest in north-east Queensland including the islands of the south-west Torres Strait, Lockerbie Scrub at the tip of Cape York, the Iron and MacIlwraith ranges, the Wet Tropics region between Cooktown and Townsville, and the Mackay area. A small population may exist even further south, near Rockhampton (Nix 1984; Schodde *et al.* 1992). The location of their non-breeding grounds in New Guinea is unclear, but specimens have been collected from lowland rainforest both north and south of the central cordillera, and on some islands off the new Guinean mainland (Bell 1981; Coates 1985; also Peabody Museum and F. Bonaccorso, Papua New Guinea Museum).

Observations of one banded pair of paradise kingfishers at a nest near Mackay suggested high site fidelity between migratory flights (Andrews *et al.* 1996). Only a few banding studies of Australian migrants have been designed to examine site fidelity, but scant

evidence suggests birds may frequently return to the same territory between years (e.g. Bell and Ford 1987; Magrath 1999).

What little we know about the breeding biology of paradise kingfishers comes from opportunistic observations of a small number of nests in different parts of their breeding range (e.g. Barnard 1911; Gill 1964; Andrews *et al.* 1991, 1996; reviewed in Higgins 1999). Soon after arriving at their breeding grounds, paradise kingfishers excavate nest cavities in termitaria, in which they are reported to lay 1–4 eggs. The incubation and fledgling periods are both about four weeks. Adults hunt invertebrates and small vertebrates, mainly from the ground and lower storeys of the forest.

The aim of the present study was to describe the breeding biology of a colour-banded population of paradise kingfishers over several successive seasons at the Iron Range National Park in Cape York. In addition, we investigated the site fidelity of breeding adults and fledglings.

## Methods

### *Study site*

Our ongoing study is situated in the Iron Range National Park, which is on the eastern side of Cape York Peninsula, in far north Queensland, Australia (12°45'S, 143°17'E). Here we present the first three years of data, collected between November 1997 and March 2000. The mean annual rainfall of the area is 2100 mm, with most rain falling between December and April (Australian Bureau of Meteorology). The vegetation is characterised by a complex mosaic of tropical rainforest, woodland and heath (Hynes and Tracey 1979). Our study site is 15 ha in area, and includes patches of semi-deciduous mesophyll vine forest and transitional vegetation; the western edge and part of the southern edge of the study site are bordered by open paddocks (cleared previously for cattle) and scrubby woodland, neither of which were used by the kingfishers. We also monitored several breeding pairs at nests that were encountered opportunistically elsewhere in the park.

### *Field methods*

#### *Nest-site selection and breeding density*

As soon as the kingfishers arrived each year, we began checking all termite mounds in the study site about once a week for signs of tunnelling and the completion of nest cavities. Each year, some mounds were not used by the kingfishers. In order to document the characteristics of suitable or preferred mounds, in a single year (1999/00) we measured the dimensions of each mound (height, and the mean of two perpendicular diameters where the mound was 'fattest'), the distance between each mound and its nearest neighbouring mound (in metres, estimated by pacing), and noted whether termites were present or absent from the mound. For nests encountered opportunistically outside the main study area, we simply noted whether termites were present and measured the dimensions of most mounds.

#### *Breeding success*

We monitored the timing and success of breeding attempts by checking the contents of nesting cavities using a small torch and a mechanic's inspection mirror. If the clutch initiation date was not known from direct observation, it was estimated by subtracting the mean incubation period of 26 days (see Results) from the hatching date. After hatching, nests were checked carefully for unhatched eggs. Other losses in productivity were attributed to brood reduction if one nestling (which was usually clearly the smallest) disappeared, and to predation if the whole clutch or brood suddenly disappeared. Fledging success was taken as the number of nestlings present on the final visit to the nest, when they were at least 22 days old (i.e. 5 days or less to fledge).

Nestlings were usually handled once, when they were old enough to band with a single numbered aluminium band. A small blood sample (20–120 µL) was taken from the brachial vein, and a molecular technique was used to identify gender from their DNA (Griffiths *et al.* 1998). Nestlings were also weighed and measured, which allowed us to estimate their age if we did not know their hatch dates from direct observation. Growth curves were calibrated using measurements from nestlings of known age. To gain access to nestlings, we cut a square plug in the wall of the termite mound with a keyhole saw. The plug was

usually about 10 cm square, and about 12 cm thick. After handling the nestlings, the plug was replaced, and securely 'cemented' in place with mud. This 'grouting' was camouflaged by rubbing dark-coloured termitaria dust onto the surface of the join. The termites reinforced the plug within days of its removal; if we wanted to access the nestlings again, we had to re-cut the plug.

Nests provided different information depending on the stage at which they were found. For example, if nestlings had already hatched, we could monitor fledging success and whole-nest predation, but we could not be sure whether brood reduction had occurred. Some nest cavities were particularly hard to see into, and we could not count eggs with confidence; these nests were excluded from the analyses of clutch size. Finally, a few nesting attempts were not completed by the time we left the study area in late February each year; we excluded these nests from analyses of fledging success and predation because we could not be sure of their final outcome. In 1999 we revisited the study site for 10 days in March, and checked every termite mound to confirm that breeding had finished.

#### *Social system and return rates*

At most nests we caught adult kingfishers by setting mist nets near the termite mound after nestlings had hatched. Captured birds were banded with a numbered aluminium band and a unique combination of plastic colour bands for individual recognition. We also censused adults using playback and a kingfisher dummy (a stuffed specimen) placed in their territory. If we were concealed in a hide, this combination elicited a strong territorial response, usually ending with the dummy being knocked off its perch.

As with nestlings, we took small blood samples from each bird so that we could confirm the sex of individuals from their DNA (Griffiths *et al.* 1998) and for future analysis of the genetic mating system. Molecular sexing confirmed that females differ reliably from males in having blue and sometimes buff webbing on their tail streamers, buff instead of white on the mantle at the back of the neck, and black streaking on the back and rump instead of pure white. These features are easily distinguished in the field. When first captured, birds could be aged as in their first year, or at least in their second year, on the basis of their plumage. One-year-old birds have brown margins to their flight feathers, wing coverts, breast and belly feathers; we found it hard to assign gender to one-year-olds from plumage, and instead relied on molecular techniques.

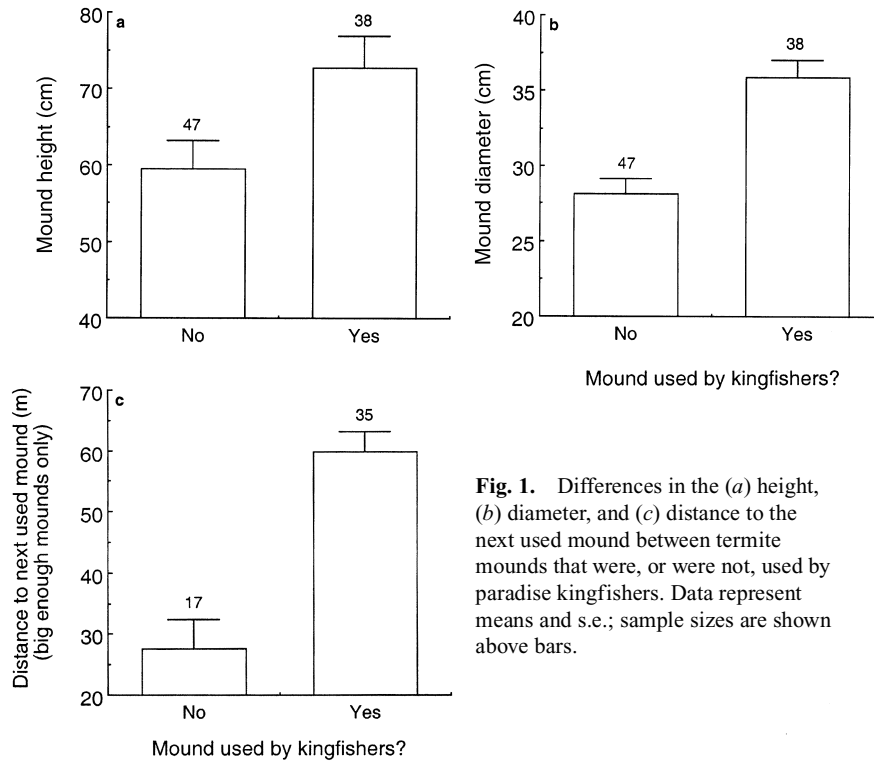
## **Results**

### *Arrival*

In all three years, paradise kingfishers appeared to arrive at the Iron Range *en masse*, at night or in the early morning; one day they appeared to be absent, but on the next could be heard calling everywhere. However, in 1998 two birds were sighted on separate occasions one week before widespread calling began (personal observation and C. Blackman, personal communication; see also Barnard 1911 for a similar observation). This suggests that their arrival may be somewhat staggered.

After arriving, birds began establishing their territories immediately, and territory owners called almost incessantly in the mornings and late afternoons. We often saw rapid chases involving 2–4 birds, and on one occasion found a male with a freshly broken wing, apparently incurred during a territorial fight. At least two other males were within a few metres of the injured male, displaying and calling, presumably trying to take over the new vacancy. Their territorial call consisted of a rhythmic, ascending series of syllables (each syllable with one or two pulses), and was usually made whilst perched in the mid to upper storey of the forest. They pointed their blue heads and orange beaks skyward, and pulled their wings down towards the ground, exposing their backs. They fluffed up the brilliant white feathers on their back and rump, beating their tail streamers in time with the calls. The first sign of tunnelling was seen in termite mounds within two weeks of the kingfisher's arrival each year.

Although we were not present at our study area during April and May, we know that in 2000 the kingfishers left Iron Range between 4 and 13 April (K. Goetze, personal communication).



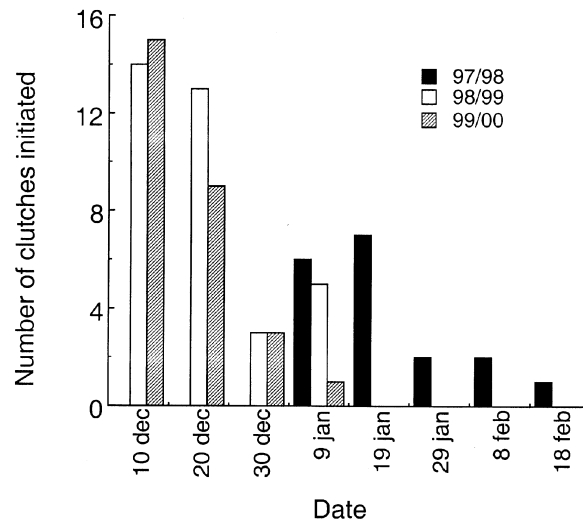
**Fig. 1.** Differences in the (a) height, (b) diameter, and (c) distance to the next used mound between termite mounds that were, or were not, used by paradise kingfishers. Data represent means and s.e.; sample sizes are shown above bars.

#### Nest-site selection

We monitored 91 nesting attempts over 3 years. The paradise kingfishers in the study area nested exclusively in termite mounds standing directly on the ground, on rotting logs, or against the base of a tree. The two highest mounds were attached to living trees with their bases 1.5–2 m off the ground.

Mounds were never used by kingfishers if termites were absent ( $n = 17$ ). This explained why 27% of 64 unused mounds in the study area in 1999/00 were avoided. Mounds were also avoided if they were small: mounds that had termites present but were still unused were significantly shorter than used mounds (mound height, ANOVA  $F_{1,83} = 5.67$ ,  $P = 0.02$ ; Fig. 1a) and less broad (mean mound diameter, ANOVA  $F_{1,83} = 23.7$ ,  $P < 0.001$ ; Fig. 1b). However, some mounds were avoided by kingfishers even though they were apparently large enough. We took all 17 unused mounds with diameters as large or larger than that of the smallest mound that was used (28.5 cm), and compared their distances to the nearest used mounds with the distances between each used mound and its nearest used neighbour. Unused mounds were significantly closer to a used mound than used mounds were to each other (ANOVA  $F_{1,50} = 28.8$ ,  $P < 0.001$ ; Fig. 1c). Thus, kingfishers avoided mounds if termites were absent, if they were too small, or if they were too close to another used mound. Using these criteria, only three out of the 64 (4.7%) unused mounds were apparently suitable.

The turnover of termite mounds between years was quite high. Of 21 mounds used and monitored in 1997/98, 41% were unusable the next year; of 35 breeding mounds monitored



**Fig. 2.** Distribution of clutch-initiation dates in each of three breeding seasons. Each season is split into 10-day intervals, and clutch initiations are counted up to, and including, the date indicated below each bar.

in 1998/99, 34% were unusable in 1999/00. Mounds became unusable because termites vacated ( $n = 11$ ), they fell over and disintegrated ( $n = 6$ ), or were partially dug out, probably by a goanna (*Varanus* sp.) or echidna (*Tachyglossus aculeatus*), and were therefore too small ( $n = 4$ ). Mound loss made it hard to assess whether the birds that had bred there the previous year had returned.

#### *Breeding dispersion*

The density of terrestrial mounds (used and unused) in the main study area was approximately  $6 \text{ ha}^{-1}$ . However, the density of territories was much smaller: we knew of 29 territories in our 15-ha study site in 1998/99, and 31 territories in 1999/2000. Thus, there were about two territories per hectare, which is less than the  $5 \text{ ha}^{-1}$  noted by Beruldsen (1990) for the tip of Cape York. In 1999/00 only 23 of the 31 territories were used for breeding. Three territories were maintained by a pair even though breeding was impossible because there were no mounds available (i.e. mounds used in previous years had fallen over, been dug out or were without termites). In the remaining five territories an unpaired male defended the territory.

#### *Laying dates*

In each season, kingfishers initiated clutches quite synchronously (Fig. 2). For example, in the 1999/2000 breeding season, over 85% of clutches were initiated within 20 days. However, there was considerable variation in clutch-initiation dates among years, with the 1997/98 season starting one month later than the following two years (Fig. 2). These differences may be explained by rainfall patterns: in the 1998/99 and 1999/00 seasons the rains started earlier than usual, and were matched by an early breeding season for the kingfishers (Fig. 3).

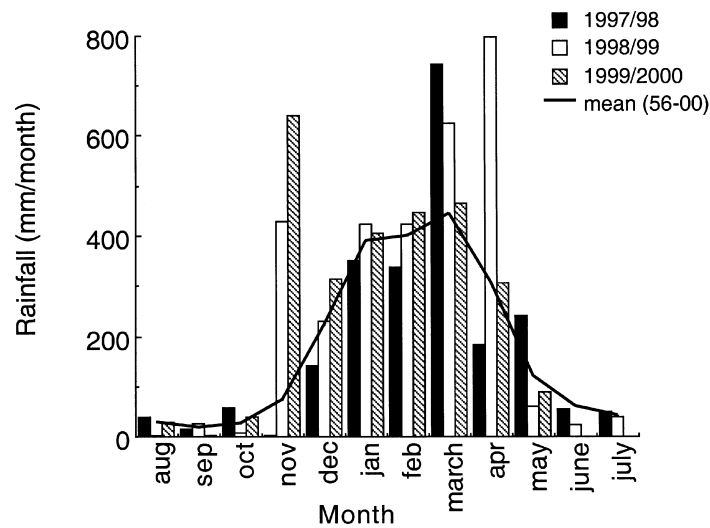


Fig. 3. Bars show the monthly rainfall (mm) for the three breeding seasons of study. The mean monthly rainfall for 1956–2000 is depicted by the solid line.

#### *Incubation and the nestling period*

We avoided visiting nests during egg-laying, but at two nests we observed that eggs were laid at daily intervals. Eggs measured  $26.8 \text{ mm} \pm 1.07$  (s.d.) in length, and  $22.8 \text{ mm} \pm 0.78$  (s.d.) in width ( $n = 8$ ). The sample is small because we preferred not to risk damaging eggs by cutting into the mound at this stage. Incubation was measured carefully in six nests, and lasted 25–26 days (mean = 25.5) from the day the first egg was laid till the day hatching began. Clutches took 1–2 days to hatch ( $n = 10$ ).

Pin feathers began emerging on nestlings seven days after hatching, and their eyes began opening after nine days, and were fully open (but milky) after 18 days. Feathers remained sheathed until one or two days before fledging, presumably to protect them from the rancid conditions in the nest; parents performed little or no nest sanitation. Once nestlings were present, the nest floor was covered with a layer of maggots. The inside of the cavity was very humid – condensation was usually evident on the walls. The wall surfaces were smooth, and there were no termites in the cavity itself. Nestlings fledged  $27.3 \pm 1.3$  (s.d.) days after hatching (range 25–30,  $n = 20$  nests).

The sex ratio of 114 nestlings over three breeding seasons was 48.2% male, and did not vary significantly between years (47.1%,  $n = 34$ ; 53.5%,  $n = 39$ , and 43.9%,  $n = 41$  in the three successive years; heterogeneity test:  $\chi^2_2 = 0.82$ ,  $P = 0.66$ ).

#### *Parental care*

We did not make systematic observations of parental care. However, both sexes were found incubating eggs and feeding nestlings. We believe that incubation and brooding bouts during the day are infrequent and short because we rarely flushed adults from the nest, despite approaching with extreme care. We avoided disturbing nests near nightfall, but on the three occasions that we flushed a bird on dusk and were able to identify it, we found it was the female. Nestlings were fed a range of invertebrates up to 3 cm in length, including cicadas, grasshoppers, beetles, stick insects, and large dipterans. We never saw the remains

of any vertebrate (e.g. skinks), although remnants of these prey may be less likely to persist in nests compared with invertebrate remains such as beetle carapaces and cicada wings.

#### *Social system*

A small proportion of nests (7%,  $n = 71$  breeding attempts) were attended by a trio of birds rather than a simple pair. The third bird was always a male; in one case he was one year old, but in the other four cases he was at least two years old. None of the helpers were seen attending the same nest the following year, but one helper was found breeding at another nest two years after his initial capture. Helpers fed nestlings, but we do not know whether they contributed towards nest excavation, incubation, or territory defence.

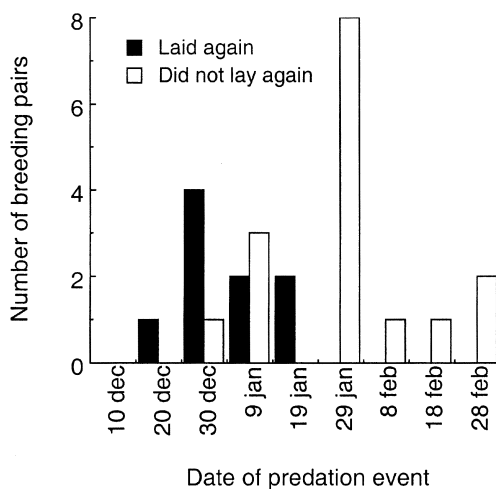
Breeders were usually at least two years old. In 71 breeding attempts, one-year-olds were found breeding in only four instances (5.6%). Nevertheless, this indicates that paradise kingfishers are sexually mature in their first year. The oldest known breeders were at least four years old: of 17 caught in 1997/98, all of which were at least two years old, 8 were still present in 1999/00.

#### *Breeding success*

Kingfishers were single-brooded (1–1.14 attempts per pair each year,  $n = 91$ ). Second clutches were laid only if the first attempt failed completely due to predation. Pairs were more likely to lay again if they lost eggs (8/16) rather than nestlings (1/9; heterogeneity test  $\chi^2_1 = 4.21$ ,  $P = 0.04$ ). This may have been because pairs had less time left in the breeding season to lay another clutch after losing nestlings (Fig. 4).

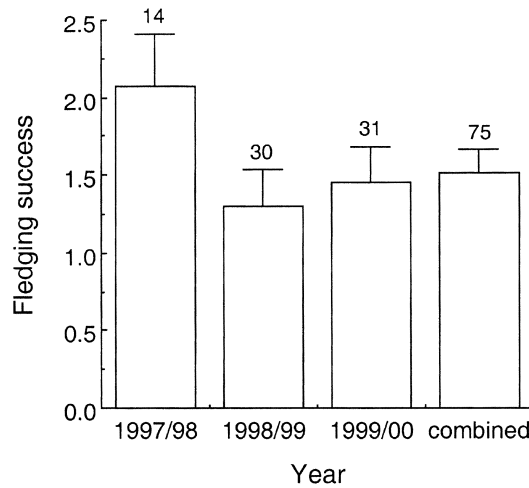
In 68 clutches where we were able to count the eggs, clutch size varied from two to three; the modal clutch size was three (82.4% of clutches). There was variation in clutch size between years, with the 1997/98 season having fewer clutches of two compared with the next two breeding seasons (clutches of 2/total clutches: 1997/98 = 0/16, 1998/99 = 8/31, 1999/2000 = 4/21, total = 12/68; heterogeneity test  $\chi^2_2 = 7.52$ ,  $P = 0.023$ ).

Over all three seasons, the mean fledging success per nest was  $1.51 \pm 1.3$  (s.d.) ( $n = 75$ ). Again, there was variation in fledging success between years, with the highest fledging success occurring in the 1997/98 season (Fig. 5). However, these differences were not significant (ANOVA  $F_{2,72} = 1.83$ ,  $P = 0.17$ ).



**Fig. 4.** Distribution of nest failures due to predation. Failed attempts that were followed up with a replacement clutch are shown separately from those where the breeding pair did not re-lay. Nest failures are summed over 10-day intervals up to, and including, the date indicated below each bar.





**Fig. 5.** Fledging success in each of the three breeding seasons, and combined. Data represent means and s.e.; sample sizes are given above bars.

The fledging success of nesting attempts was reduced by three factors: hatching failure, brood reduction, and predation. Hatching failure was generally low: just 3.2% of 158 eggs failed to hatch (in 5/60 clutches). Hatching failure was not more prevalent in some years than others (heterogeneity test  $\chi^2_2 = 0.05$ ,  $P = 0.98$ ; Table 1). Brood reduction occurred in 24% of nests with young ( $n = 50$ ) over three breeding seasons. Although fewer nests suffered brood reduction in 1997/98, this difference was not significant, perhaps because the sample of nests for 1997/98 was relatively small (heterogeneity test:  $\chi^2_2 = 2.70$ ,  $P = 0.26$ ; Table 1). We also examined the number of nestlings that died from brood reduction, because although similar numbers of nests were affected each year, breeding pairs could lose two nestlings rather than just one in a poor year. Overall, 10.6% of nestlings ( $n = 132$ ) died from brood reduction, and although the mortality rate per nestling in 1997/98 was lower (3%), this difference was not significant (heterogeneity test:  $\chi^2_2 = 3.55$ ,  $P = 0.17$ ; Table 1). Predation resulted in the complete failure of 33% of breeding attempts ( $n = 76$ ). Predation rates were lowest in the 1997/98 breeding season, and highest in 1998/99, although, once again, this difference was not significant (heterogeneity test:  $\chi^2_2 = 2.22$ ,  $P = 0.33$ ; Table 1).

**Table 1. Causes of productivity loss during nesting attempts**

Incidence of hatch failure (per egg), brood reduction (per nestling and per brood), and predation (per attempt) in three breeding seasons. Numbers in parentheses represent sample of egg, nestlings, broods or attempts

	Hatch failure (%)	Brood reduction		Predation (attempts) (%)
		Nestlings (%)	Broods (%)	
1997/98	2.6 (38)	3 (32)	8 (12)	21.4 (14)
1998/99	3.3 (60)	11 (47)	28 (18)	41.9 (31)
1999/2000	3.3 (60)	15 (53)	30 (20)	29 (31)
Total	3.2 (158)	11 (132)	24 (50)	33 (76)

### *Return rates*

The return rate of breeding adults between years was high but variable. Between 1997/98 and 1998/99 84% of banded adults returned to the study area ( $n = 19$ ). However, between the 1998/99 and 1999/00 seasons, only 56% of banded adults returned ( $n = 40$ ). Combining the data from both years, the annual return rates for males and females were similar (males = 68%,  $n = 31$ ; females = 61%,  $n = 31$ ). Note that the sample used here does not include all the adults we banded at the site (77) because some birds were banded in the third year of study, and we were unable to check all the territories each year (for example, because flooding prevented access).

Most returning birds settled on the same territory they had occupied the previous year; only 3 returning birds (7.9%,  $n = 38$ ) moved territories. All were females that had been 'widowed', with their previous partner failing to return.

In contrast to breeding adults, only one bird banded as a nestling (1.5%,  $n = 66$ ) was observed to return and breed within the same area; she moved 1200 m from her natal territory to her breeding territory.

## **Discussion**

### *Arrival and timing of breeding*

At the Iron Range National Park, the arrival and breeding times of paradise kingfishers were apparently timed to match the onset of the wet season. For example, in 1998 and 1999 the rains came several weeks earlier than in 1997, and the kingfishers began breeding correspondingly earlier. Anecdotal observations in the literature support the link between rainfall and migration. For example, in 1911 kingfishers arrived at the tip of Cape York as late as 23 November, and Barnard (1911) noted that it had been a very dry year. In other parts of their Australian range, paradise kingfishers have arrived as early as 12 October (Gill 1970). Thus the arrival times of the kingfishers are labile.

Paradise kingfishers may breed at the start of the wet season to take advantage of increases in the abundance of leaf litter invertebrates. The other breeding migrant to the Iron Range that specialises on leaf litter invertebrates (*Pitta erythrogaster*) also arrives with or just after the paradise kingfishers and breeds at the same time (personal observation). There have been no studies of seasonal invertebrate abundance in the Iron Range area, but large fluctuations in abundance have been noted in other tropical forests (Fogden 1972; Levings and Windsor 1982; Frith and Frith 1990).

### *Nest-site selection*

Although arboreal termite mounds were present at our study site, the mounds used by the paradise kingfishers were always terrestrial. Kingfishers are also found in rainforest adjacent to major rivers where prolonged inundations make terrestrial termitaria extremely scarce, so they may use arboreal mounds in these areas. However, they are likely to face stiff competition with the yellow-billed kingfisher (*Syma torotoro*), a year-round resident that prefers to nest in arboreal mounds and establishes its territories earlier (September, personal observation).

The paradise kingfishers never nested in inactive termite mounds (see also MacGillivray 1914). Mounds become considerably more unstable and friable after the termites leave, probably making it easier for predators to break into the mound, and more likely that the mound will disintegrate. In addition, the temperature inside nest cavities may be more stable if termites are present, freeing the kingfishers from some incubation duties (e.g. Lill

and Fell 1997). Although we did not observe incubation behaviour by parents systematically, we noticed that clutches were rarely incubated by adults during the day. If termites maintain the temperature inside mounds near the incubation optimum (36–38°C), this would also explain the low level of hatch failure in this population (3.2%), since eggs would rarely be exposed to ambient temperatures outside the mound which are likely to be below the incubation optimum but above physiological zero (24–27°C). These temperatures can result in developmental failure (Stoleson and Beissinger 1999), and may explain why hatching failure at lower latitudes exceeds that of temperate areas (Koenig 1982; but see Skutch 1985).

#### *Breeding success*

Pairs of paradise kingfishers fledged an average of 1.5 young per year, which is less than that reported for the common paradise kingfisher in New Guinea, where the fledging success per pair was at least three (Bell 1980). This may reflect larger clutch sizes for the latter species (Coates 1985).

During this study, the breeding success of paradise kingfishers was affected mainly by predation, which terminated one third of attempts. This failure rate is similar to that reported for hole-nesters in other lowland tropical forests, for example 22% in Papua New Guinea (Bell 1982), and 33% in the neotropics (Skutch 1985). The main predators at Iron Range were probably snakes with slender builds (e.g. *Dendrelaphis calligastra*, *D. punctulata*, *Boiga irregularis*) or possibly small goannas (*Varanus* sp.). Most birds, mammals and larger goannas would need to widen the nest tunnel to reach the cavity, but we rarely observed such damage. In a single instance a black butcherbird (*Cracticus quoyi*) broke the wall of a mound to reach the cavity – this mound was small and the walls were unusually thin. The rarity of avian and mammalian predation illustrates the benefits of hole-nesting, since many types of predators are unable to gain access to the nest. Predation is generally more severe for open-cup nesters than for hole-nesters, especially those that excavate their own holes (Martin and Li 1992).

Variation in predation pressure has often been invoked to explain different life-history strategies of tropical versus north temperate, and open- versus hole-nesting birds. Compared with north temperate species, tropical species have been characterised as being long-lived, and laying small but multiple clutches, as a result of higher nest predation (Skutch 1985; Martin 1993, 1996; see also Rowley and Russell 1993). However, several recent studies have questioned these dogmas, showing that nest predation, longevity, and the number of broods are not necessarily higher in the tropics (Karr *et al.* 1990; Martin 1996; Martin *et al.* 2000). Similarly, in the study reported here, nest predation was relatively low and breeding pairs were essentially single-brooded, yet they still laid small clutches. Although we are cautious about inferring too much from a single-species study, our data do run counter to the idea that nest predation and multiple broods explain the small clutches of tropical species. The ‘life-history’ debate is hampered by scant empirical data from tropical regions (Martin 1996). Within Australia, intensive studies of avian breeding biology are dominated by temperate and coastal-living species (Clarke 1997), and more data from the tropical regions are required before the relationships between life-history attributes can be resolved.

Partial brood reduction occurred in one quarter of paradise kingfisher broods. Brood reduction appears to be a fairly widespread phenomenon in kingfishers (Fry *et al.* 1992), probably due to two factors. Most kingfishers hatch their young asynchronously, creating a size and dominance hierarchy in the brood. Also, all kingfishers nest in holes, allowing

dominant chicks to monopolise access to food by physically occupying the tunnel entrance (see Legge 2000 for a detailed example in kookaburras, and Anderson *et al.* 1993 for a similar example in raptors). Thus, resource allocation between chicks can quickly become uneven and lead to the selective starvation of the weakest chick. Food availability may be a critical factor limiting reproduction in tropical birds (e.g. Thiollay 1988), in contrast to a common perception that rainforests provide abundant and stable food resources.

#### *Social system*

Like most kingfishers (Fry *et al.* 1992) the paradise kingfishers in this study were intensely territorial, responding vigorously to the calls and intrusions of other birds. Even in the few cases where territories lacked mounds suitable for nesting (e.g. because the mound used previously had fallen over), the resident kingfishers defended their territories throughout the breeding season, returning again the following year after the mounds had been repaired by the termites to resume breeding. This suggests that termite mounds limit breeding opportunities, and are a particularly valuable resource to the kingfishers.

The paradise kingfishers in this study formed long-term pair bonds, with both sexes showing high fidelity to their partner and territory between years. Only three out of 40 returning birds moved territories and paired with a new partner – in each case their previous partner failed to return and was presumed to be dead. Social monogamy is probably the norm for kingfishers in general, although there have been few studies detailed enough to reach firm conclusions (Fry *et al.* 1992). A small proportion of paradise kingfisher pairs (7%) were accompanied by an extra male who helped to provision the young. This confirms Dow's suspicion (1980) that the species may be cooperative. Helpers in most cooperatively breeding birds are offspring from previous breeding attempts that benefit through inclusive fitness (e.g. Legge and Cockburn 2000). However, paradise kingfisher helpers may be unrelated to the pair they assisted because none of the males we banded as nestlings returned to the study area. Unpaired males may still accrue direct benefits from helping an unrelated pair, including access to the breeding female and female fledglings (Reyer 1990; Sherley 1990; Whittingham *et al.* 1997). Breeding males may tolerate the presence of a helper on the territory if the latter assists with territory defence or increases fledging success. Our planned molecular analysis of parentage is partly aimed at resolving whether reproductive conflict exists between the resident group males.

#### *Return rates*

Between 56 and 84% of banded adults returned between one year and the next, yielding an annual mortality rate of 26–44%. We cannot explain the differences observed among years, but they may relate to conditions experienced on the staging or non-breeding grounds. Given that breeding pairs fledged only 1.5 young per year, and many immatures are likely to die before being recruited into the breeding population, these mortality estimates seem a little high. We may have overestimated mortality if some banded birds resettled outside our study area. However, similar figures were reported for a small number of common paradise kingfishers in New Guinea (67–75% of adults survived between years: Bell 1980). In contrast, annual survival rates for four species of forest-dwelling kingfishers in Sarawak, including one migratory species, were 83–100% (Fogden 1972) although, once again, the sample sizes were low.

Although the return rates of adult male and female paradise kingfishers were not significantly different, demographic observations indicated that there may be differences in migratory behaviour and/or costs between the sexes. For example, all the one-year-old

breeders we observed were females, and five territories were defended vigorously by unpaired males in one year. This suggests that females were in relatively short supply on the breeding grounds, but more data on return rates are required to test this.

The recruitment of birds into the study area that were banded as nestlings was low (1.5%). This suggests low natal philopatry of sons as well as daughters, which would be unusual for birds (Greenwood 1980). However, the study area is small (15 ha) and recruits may have settled successfully nearby. In addition, it is possible that some young birds defer migration back to the breeding grounds until their second year, in which case we may encounter more recruits in later years of the study.

### *Migratory patterns*

The location of the non-breeding grounds for paradise kingfishers in New Guinea is unknown, but specimens have been collected from the watersheds both north and south of the main mountain ranges (Bell 1981; Coates 1985; Peabody Museum; F. Bonaccorso, Papua New Guinea Museum; R. Schodde, CSIRO). The southern watershed of New Guinea and Cape York share a common weather system, except that New Guinea experiences the wet season rains slightly earlier. If paradise kingfishers aim to migrate and initiate breeding at the start of the wet season in Cape York, as seems likely from the data presented here, the first stormy weather in the southern watershed of New Guinea could provide an accurate cue for kingfishers to begin their migration south. In contrast, the weather systems of the northern watershed are not linked to those in north-east Queensland, and it is less clear what cues paradise kingfishers could use there to time their migration. However, if the breeding populations in Australia are drawn from the northern as well as the southern watershed, this could explain the reputed differences in arrival dates for the paradise kingfishers in different parts of their Australian range (e.g. Officer 1967).

In summary, we have described the breeding biology of the buff-breasted paradise kingfisher using data drawn from a large sample of nests. Such information from tropical birds is scarce, and therefore particularly valuable for unravelling the differences in life-history strategies of tropical versus temperate, and open- versus hole-nesting birds. In addition, we have shown that adults are faithful to their breeding territory and partner between migratory flights. However, we still know little about their distribution and habits during the non-breeding season. As the lowland rainforests of New Guinea come under increasing threat from logging and other development (Sizer and Plouvier 2000), information on the migratory patterns and off-season requirements of many trans-Torres migrants may prove crucial for their conservation.

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