

SEASONAL PATTERNS OF REPRODUCTION IN HEATHLAND HONEYEATERS ARE NOT RESPONSES TO CHANGING NECTAR AVAILABILITY

DOUG P. ARMSTRONG^{1,2} AND GRAHAM H. PYKE²

¹*School of Biological Sciences A08, University of Sydney, New South Wales 2006, Australia, and*

²*Division of Environmental Sciences, The Australian Museum, 6-8 College Street, Sydney, New South Wales 2000, Australia*

ABSTRACT.—We monitored nesting attempts of New Holland (*Phylidonyris novaehollandiae*) and White-cheeked (*P. nigra*) honeyeaters on two sites throughout 1987 and 1988. Two aspects of the birds' reproduction were correlated with changes in availability of nectar. First, breeding periods of both species were centered on the winter peak of nectar availability. Second, all clutches laid in the first two months of the breeding period failed, and this was the portion of the breeding period when nectar was scarcest. We tested whether these seasonal patterns were caused by changes in availability of food energy by supplying birds on one site with continuous access to sugar-water feeders for 9 months starting in January 1988. Seasonal patterns of nesting effort and nest success were similar for birds on the two sites, and were similar to patterns observed in 1987. We therefore conclude that these patterns were not caused by seasonal changes in availability of food energy. Circumstantial evidence indicated that snake predation may have accounted for most early nest failures. We suggest that predation—rather than scarcity of nectar—may prevent breeding over the warmer months of the year. Received 24 August 1989, accepted 23 July 1990.

AVAILABILITY of food energy could limit avian reproduction in several ways. It could limit the proportion of birds that breed, the duration of breeding periods, the numbers of broods reared during those periods, the sizes of clutches, and the survivorship of clutches and broods. If given access to extra food, several bird species will breed earlier and may lay larger clutches or additional clutches (Martin 1987, Daan et al. 1988). Previous supplementation experiments have involved carnivorous or granivorous birds, so it is not clear whether reproduction was limited by availability of energy or solely by availability of other nutrients, such as protein.

Some nectar-feeding birds derive most of their dietary energy from nectar and get all their other nutrients from insects (Pyke 1980, Paton 1982). Consequently, these birds' energy sources can be monitored and manipulated independently of their sources of other nutrients. Studies of nectar-feeding birds have found correlations between the timing of flowering and breeding periods (Rooke 1979, Ford 1980, Paton 1985, Sagar 1985, McFarland 1986, van Riper 1987) and between the amount of nectar on birds' territories and their reproductive success (van Riper 1984).

On coastal heathland near Sydney, Australia, there is a strong seasonal correlation between

the number of nesting honeyeaters (Meliphagidae) and the amount of nectar-energy produced per unit area per day (Pyke and Recher 1986, Pyke et al. 1990). New Holland Honeyeaters (*Phylidonyris novaehollandiae*) and White-cheeked Honeyeaters (*P. nigra*) account for 95% of the honeyeater nests (Pyke and Recher 1986). The breeding periods of both species are centered on the winter flowering of *Banksia ericifolia*, which produces most of its inflorescences between late April and early August (Pyke 1988, Armstrong 1991a). *Banksia ericifolia* produces by far the most nectar per area of any plant species used by the honeyeaters (Pyke 1983, 1988; Pyke and Recher 1986), and its flowering accounts for most of the seasonal variation in nectar standing crop (Armstrong 1991a).

Other than nectar, small insects are the only food items consumed frequently by New Holland and White-cheeked honeyeaters in heathland near Sydney (Recher and Abbot 1970, Recher 1977, Paton 1982, Armstrong 1991a). Insect abundance is at its lowest in winter (Pyke 1983, 1985), and is therefore inversely correlated with both availability of nectar and nesting of honeyeaters. It is unlikely that honeyeater breeding periods are determined by abundance of insects.

Although the correspondence between

breeding and flowering suggests that birds are responding to changes in availability of energy, they could be responding to a variety of other seasonal changes unrelated to flowering. We monitored nesting of New Holland and White-cheeked honeyeaters to determine seasonal patterns in proportions of resident birds that breed, clutch sizes, durations of nesting cycles, and nest success. We related these to seasonal changes in availability of nectar energy. We then used energy supplementation to determine whether those patterns that correlated with changes in nectar availability are caused by changes in availability of dietary energy.

METHODS

Study area.—We studied New Holland and White-cheeked honeyeaters in 1987 and 1988 on two patches of coastal heath in Brisbane Water National Park, New South Wales (33°32'S, 151°17'E), 35 km N of Sydney. The two sites are 11 ha (Site 1) and 4 ha (Site 2), and are separated by 500 m of dry sclerophyll forest. Site 1 is also called "Recher Heath" and has been used for several previous studies (Pyke 1983, 1988; Pyke and Recher 1986; Pyke et al. 1989, 1991). Site 2 was established specifically for this study. New Holland and White-cheeked honeyeaters resident on one of the sites are not normally seen on the other.

The birds.—Both species breed as monogamous pairs (Recher 1977, Rooke 1979, Paton 1985, McFarland 1986), and nest within territories defended by the males (Rooke 1979, Paton 1985, McFarland 1986, Armstrong 1991b). On our sites, male New Holland Honeyeaters are found on their territories year-round, and male White-cheeked Honeyeaters during all months except November and December. Females of both species are present only while breeding, and show a much higher turnover than males. Of 20 territorial males we began observing early in 1987, 15 still had territories in the same locations at the end of the 1988 breeding period. In contrast, only four of the females initially mated with those males were present at the end of the 1988 breeding period.

Both species are sexually monomorphic in plumage, but can be sexed from skull measurements (Rooke 1976, Pyke et al. 1989) or behavior of breeding pairs. We initially sexed birds from skull measurements, and confirmed sexes by noting which member of each pair incubated. Rooke (1979) sexed New Holland Honeyeaters by laparotomy, and observed that only females incubated. We assumed this to be the case for White-cheeked Honeyeaters as well. We identified all individuals by color bands.

Collection of breeding data.—We monitored nesting by conducting regular observations on males' territories. We mapped positions of resident males on both

sites in January each year, then followed the breeding attempts by those males and their mates throughout the year. In 1987, we observed territories of 8 New Holland Honeyeaters and 4 White-cheeked Honeyeaters on Site 1, and 4 New Holland Honeyeaters and 4 White-cheeked Honeyeaters on Site 2. In 1988, we observed territories of 10 New Holland Honeyeaters and 4 White-cheeked Honeyeaters on Site 1, and 5 New Holland Honeyeaters and 4 White-cheeked Honeyeaters on Site 2. We excluded two males that abandoned their territories (or died) early in the breeding period in 1988.

Regular observations of birds began after the first pair bonds formed each year, and continued until most pairs had separated. Three or four 30-min observation sessions were conducted per territory per month from February to October 1987 and from February to September 1988. Most nests were found in these sessions, but an extra 30-min session was conducted each fortnight on any pair whose nest had not been found and who had not fledged young during the past week. All observation sessions were conducted by Armstrong.

After nests were found, they were checked every 1–4 days until they failed or the young fledged (i.e. left the nest). It was easy to determine whether young had fledged by observing the area near the nest and listening for begging calls. We classified nests as successful if one or more young fledged, and unsuccessful otherwise. When measuring nest success, we included only those nests that were found before the eggs hatched.

Measurements of nectar availability.—We measured nectar availability in terms of standing crop of nectar energy (kJ/ha). We estimated the standing crop of nectar energy from densities of productive flowers and inflorescences of plant species used by birds, and from the amount of energy per flower or inflorescence of each species (Armstrong 1991a).

Energy supplementation.—The energy available to some birds was supplemented in 1988 by feeders that dispensed 25% (W/W) sugar-water solutions. We initially attempted to give selected birds on both sites access to hidden feeders in order to avoid confounding the effects of feeders and sites. However, hidden feeders were quickly discovered by non-target individuals. Consequently, we placed feeders on only one site and compared the reproduction of the birds on the two sites. We placed 14 feeders on Site 2 from 4 to 11 January, then left them there continually from 25 January until all birds finished nesting. Feeders were refilled every 48 h or less, and birds never went a whole day without access to sugar water.

We initially introduced birds to bright red hummingbird feeders (Perky Pet Brand) which we placed on Site 2 for short periods regularly in 1986 and 1987. In 1988 we switched to large (2 l) drip feeders made from plastic juice containers. We placed each feeder at least 30 m from the center of any male's territory

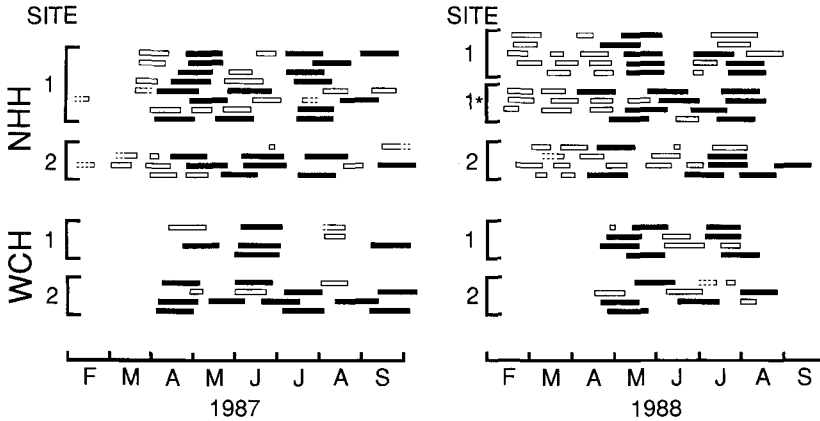


Fig. 1. Nesting attempts by New Holland (NHH) and White-cheeked (WCH) honeyeaters on sites 1 and 2. Each row indicates nesting attempts involving a single territorial male over the course of the year. Bars show successful (black) and unsuccessful (white) nests, and the extremities of each bar show dates of egg laying and fledging or nest failure. Most laying dates were estimated from hatching dates by assuming a hatching period of 14 days; broken lines indicate dates that could not be specified to within 7 days. In 1988, birds on Site 2 had access to sugar-water feeders from January to October. Some birds (*) on Site 1 flew 500 m to Site 2 to use feeders, whereas other birds on Site 1 did not use feeders.

to minimize the effect of feeders on territory intrusion rates. However, there was at least one feeder within 50 m of each territory so that the birds had easy access.

RESULTS

Over 1987 and 1988, we found 116 New Holland Honeyeater nests and 41 White-cheeked Honeyeater nests on territories that were observed regularly. We found 25 during nest buildings, 73 with eggs, and 18 with nestlings. Three New Holland Honeyeater broods and two White-cheeked Honeyeater broods fledged before their nests were found in 1987, but none did so in 1988 (broods were obvious after they fledged because of their begging calls). Some nests probably failed before they were found. However, we probably missed few nests in 1988 given that most were found within a few days of egg laying.

The two species built similar cup-shaped nests. Nests were constructed from small sticks and spider webbing, and were lined mainly with bracts from *Banksia* inflorescences and achenes from *Isopogon* inflorescences. New Holland Honeyeater nests were 0.3–3.0 m from the ground (median 0.7) and White-cheeked Honeyeater nests were 0.25–0.9 m from the ground (median 0.4). Nests were supported either by a single plant (16 different genera used) or a mixture of low heathland plants. All nests were used only once.

Seasonal patterns of reproduction.—In 1987, New Holland Honeyeaters laid clutches from mid-February to early September, and White-cheeked Honeyeaters laid clutches from early April to early September (Fig. 1). The number of clutches laid per territorial male over the year ranged from one to seven for New Holland Honeyeaters and one to four for White-cheeked Honeyeaters. Most New Holland Honeyeaters started nests by late March and continued through mid-August, and most White-cheeked Honeyeaters started nests by mid-April and continued through mid-August. Consequently, there was little variation in numbers of birds nesting over these periods (Fig. 2). Two males did not nest until late in the breeding period in 1987 (a New Holland Honeyeater on Site 2 and a White-cheeked Honeyeater on Site 1; Fig. 1). These males were previously unpaired.

All clutches of both species had two eggs, so there was no seasonal variation in clutch size. Eggs were laid either on the same day or on successive days. We measured hatching periods for all clutches for which we knew laying and hatching dates to within two days, and fledging periods for all broods for which we knew hatching and fledging dates to within two days. The midrange of possible hatching periods ranged from 13 to 15 days (median = 14) in 11 New Holland Honeyeater clutches and 13.5 to 14.5 days in two White-cheeked Honeyeater clutch-

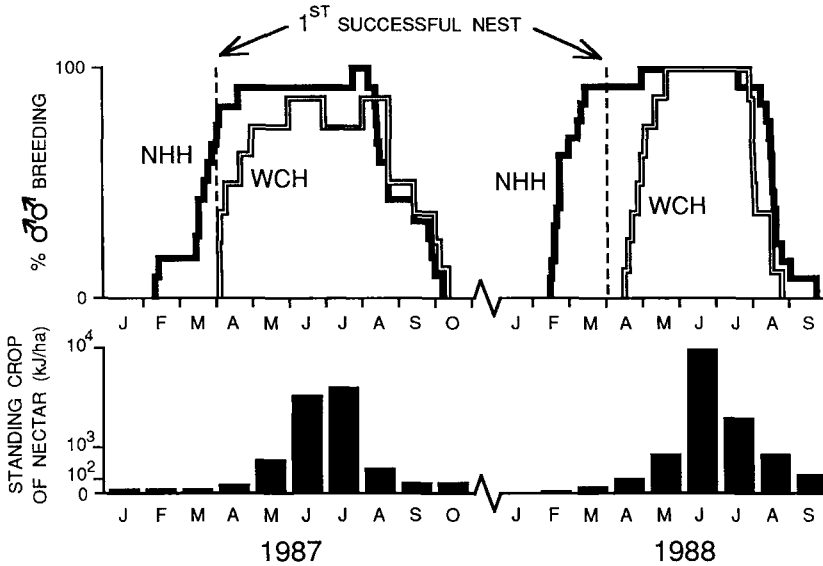


Fig. 2. Summary of nesting seasons and dates on which first successful clutches were laid in relation to seasonal changes in availability of nectar. Upward steps indicate dates of egg laying for each territorial male's first clutch of the year. Downward steps indicate dates of fledging or nest failure for each male's last clutch of the year. Measurements of nectar standing crop are monthly averages from Armstrong (1991a).

es. The midrange of possible fledging periods ranged from 12 to 16.5 days (median = 14) in 16 New Holland Honeyeater broods and 13 to 15.5 days in six White-cheeked Honeyeater broods.

We did not measure seasonal variation in incubation period, nestling period, and lag time between nests because we could not measure all these durations for most nests. However, we could usually measure the duration of the entire nesting cycle as either the length of time between laying of successive clutches or hatching of successive clutches. We measured variation in duration of nesting cycles using all cases in which we could specify one of these intervals to within one week. Males who changed mates between nests often had a lag period before they acquired another mate, and therefore they had significantly longer nesting cycles (*t*-test; $P < 0.001$). Consequently, we used only cases in which pairs stayed together between nest attempts. We classified these data according to the fate of the nest (failed before hatching, failed after hatching, or successful) and the month in which the eggs were laid. Duration of nesting cycles varied significantly with both the fate of the nest and the month (2-way ANOVA; $P < 0.05$), and there was no interaction between

these variables. The median duration of nesting cycles for successful nests increased from 43 days for clutches laid before 1 May to 60 days after 1 May, and for unsuccessful nests increased from 27 days to 34 days (Fig. 1). There were no significant differences between sites, species, or individual males ($P > 0.25$).

There was a strong seasonal change in nest success. All 11 clutches laid before 1 April failed, whereas 25 of 44 clutches laid after 1 April produced one or more young that fledged ($G^2 = 23.8$, $P = 0.001$; Fig. 1). The success rate did not vary among months from April to September ($G^2 = 6.4$, $P = 0.268$). Success rate did not differ between nests found before and after laying ($G^2 = 0.26$, $P = 0.613$), nor did it differ between sites, species, or individual males ($P > 0.25$). Both of the young fledged from 19 of the 25 successful nests, and the six nests from which only one young fledged were distributed evenly across months, sites, and species.

Of the above patterns, two corresponded predictably with changes in availability of nectar. First, breeding periods were centered on the period of peak nectar availability (Fig. 2). Second, all clutches laid before 1 April failed, and nectar was scarcest during those months (Fig. 2). Changes in duration of nesting cycles did

not correspond predictably with changes in availability of nectar, for nesting cycles were shortest early in the breeding period when nectar was relatively scarce.

Effect of energy supplementation.—In 1988, we compared reproduction of birds with continuous access to sugar water with birds whose access to energy varied with seasonal changes in nectar availability. All birds observed on Site 2 used feeders regularly when nectar was scarce. In addition, both members of four pairs of New Holland Honeyeaters from Site 1 visited feeders several times. No other birds from Site 1 used feeders in 33 h of observations in 1988. Consequently we categorized New Holland Honeyeater pairs into three groups: those that used feeders within 50 m, those that used feeders ca. 500 m away, and those that did not use feeders.

There were no differences in the breeding periods of the three groups of New Holland Honeyeaters, nor were there any differences between White-cheeked Honeyeaters on Site 1 and Site 2 (Figs. 1, 2). Most New Holland Honeyeaters started nests by late February in 1988, and the median date on which first clutches were laid was 30 days earlier than in 1987. Most White-cheeked Honeyeaters did not begin nests until late April in 1988, hence the difference was more pronounced between the breeding periods of the two species in 1988 than in 1987. Most birds of both species finished nesting in August 1988.

Seasonal patterns of nest success in 1988 were almost identical to those observed in 1987 for all groups of birds (Fig. 1). All 20 clutches laid before 1 April failed, whereas 31 of 59 clutches laid after 1 April produced one or more young that fledged ($G^2 = 39.2$, $P < 0.001$). Of 7 other clutches laid before 1 April by birds that were not monitored regularly, 1 was successful. This nest was atypical as it was 3 m high (twice as high as any other nest). The seasonal increase in success rate was significant for all three groups of New Holland Honeyeaters ($P < 0.01$). Success rate did not vary among months from April to August ($G^2 = 5.4$, $P = 0.145$). During this period, there were no differences between species or between different groups in either species ($P > 0.25$).

All nests had two eggs in 1988, except for a three-egg clutch laid by a pair of New Holland Honeyeaters on Site 2. Duration of nesting cycles varied only with the fate of nests in 1988; there was no additional variation in duration

TABLE 1. Fate of eggs or nestlings in failed nests.

Gone from nest	70
Killed by storm	11
Killed by fire	1
Eggs infertile	3
Abandoned	2
Infested with fly larvae	2
Dead: no apparent cause	2

of nesting cycles among months (2-way ANOVA; $P = 0.354$), or between species or sites ($P > 0.50$).

Circumstances of nest failures.—We recorded 91 nest failures over 1987 and 1988 (Table 1). We considered nest failure to have occurred when the last egg or nestling died or disappeared. Of the 91 nests, 70 were empty or contained remains of eggs or nestlings. The nestlings or embryos in 11 nests died or were washed through their nests during heavy rain, and one nest was destroyed by fire. Three nests had infertile eggs, two had nestlings that died after they were abandoned, and two had dead nestlings with heavy infestations of subcutaneous maggots (*Passeromyia indecora*; references to this parasite in Hindwood 1930 and Pont 1974). In the two remaining cases, nestlings or embryos were found dead and there was no apparent cause of death.

Of the 70 nests whose contents were eaten or otherwise disappeared, young most commonly disappeared without a trace shortly after hatching. The eggs were known to have hatched in 41 cases, may or may not have hatched in 18 cases, and had not yet hatched in 11 cases (assuming an incubation period of 14 days). In only 10 cases, nestlings disappeared a week or more after hatching; and no nestlings that hatched before mid-April (i.e. from clutches laid before 1 April) survived that long. There were obvious signs of predation at only 4 of 30 nests (13%) whose contents disappeared before mid-April, and at 15 of 40 nests (38%) whose contents disappeared later. The signs of predation included pieces of eggshell or nestling (8 nests), and tilting of nests, disturbance of nest lining, or both (11 nests). One of the disturbed nests had a rat (*Rattus* sp.) dropping on the brim.

From February to April 1988, we checked nests at dawn and dusk whenever possible to determine when contents disappeared. Eggs disappeared between dawn and dusk on 2 of 4 occasions, and nestlings disappeared between dawn and dusk on 2 of 11 occasions. One brood

that was gone at dusk had been there 30 min earlier. The other brood had only one nestling, which earlier appeared very weak, and probably died before it was removed.

DISCUSSION

Of the four aspects of reproductive output we measured, two aspects were correlated predictably with seasonal changes in nectar availability. First, breeding periods were centered on the peak of nectar availability (June or July). Second, all clutches that were laid in February and March (when nectar was scarcest) failed.

Despite these seasonal correlations between nectar availability and reproductive output, energy supplementation had no effect on either breeding periods or nest success. Food supplementation experiments on other bird species have produced such effects, particularly earlier initiation of nesting (Martin 1987, Daan et al. 1988). However, we know of no experiments that show effects of energy supplementation on reproductive output of nectar-feeding birds. Van Riper (1984) found that Common Amakihi (Drepanidinae: *Hemignathus virens*) nested in a normally unoccupied area when sugar-water feeders were available. However, it is not known whether the birds involved would have nested elsewhere, and whether the feeders increased their reproduction.

Breeding periods of New Holland Honeyeaters have been monitored in other locations (Rooke 1979, Ford 1980, Paton 1985, McFarland 1986), and in all cases breeding periods appear limited by energy availability. These authors found peaks of breeding activity in autumn (February to May), spring (July to October), or both. These peaks corresponded to peak availability of nectar or other carbohydrate sources (manna, honeydew). Only in our study did New Holland Honeyeaters breed extensively throughout winter.

From previous research at Site 1, Pyke and Recher (1986) suggested that New Holland and White-cheeked honeyeaters start and stop nesting when production of nectar energy reaches some critical threshold needed for nesting. This hypothesis was not supported by the responses of the birds to energy supplementation. They did not nest either earlier or later when they had continuous access to sugar water. It is unlikely that feeders did not adequately supplement energy to birds. All birds observed on Site

2 used feeders regularly and rarely visited flowers when nectar was scarce (Armstrong 1990). Birds had quick access to feeders, and were rarely excluded by aggressive interaction (Armstrong 1990). Consequently, the proportion of time they spent feeding on carbohydrate sources remained at low levels throughout the breeding period. For birds without access to feeders, the proportion of time spent foraging in March, September, and October was three to four times higher than it was from May to July (Armstrong 1991a).

New Holland Honeyeaters on Site 2 had continuous access to feeders for only about 6 weeks before they started nesting, and this period may have been too short to affect onset of breeding. It is unlikely that nesting earlier in 1988 than in 1987 was related to feeders, for the earliest nesting occurred in birds that did not use feeders. We may have missed the first nests of some New Holland Honeyeaters in 1987, so the difference in their onset of breeding between years may not have been as pronounced as shown (Figs. 1, 2). White-cheeked Honeyeaters on Site 2 did not nest until late April and should have had ample time to adjust the onset of nesting if it were related to changes in availability of energy. Both species stopped breeding at the end of winter even though feeders continued to be available.

Energy supplementation provided strong evidence that seasonal changes in nest success were unrelated to changes in energy availability. All seven clutches that were laid on Site 2 before 1 April in 1988 failed, even though the four pairs involved had continuous access to sugar water. In contrast, 7 of 14 clutches they laid later in the year were successful. Circumstances of nest failures also indicate that seasonal changes in nest success were not caused by changes in energy availability. If nest failure was due to insufficient energy availability, then embryos would die from insufficient incubation or nestlings would die from insufficient brooding or lack of food. If this were the case, dead embryos or nestlings would often be found in nests early in the year.

On the contrary, most eggs or nestlings disappeared from nests and were probably taken by predators. It is unlikely that nestlings fell from nests or that non-viable eggs or dead nestlings were removed by parents, unless they continued to use the nests. In those cases in which dead embryos or nestlings were found, death

could usually be attributed to storms or parasitism. Nestlings were abandoned in two cases, but neither case could be attributed to insufficient energy, for they occurred when nectar was abundant. The parents never returned in one case, and may have died. In the second case, one nestling was missing and the nest was covered with adult feathers. Neither parent was killed, but they probably abandoned the nest after an attack by a predator. Of two cases in which the cause of death was not apparent, one occurred when nectar availability was at its peak. The other case, in which a pair of embryos died in late February, is the only nest failure that could be easily attributed to insufficient energy.

Early in the breeding period nestlings most commonly disappeared from the nest shortly after hatching. Most disappeared without a trace between dusk and dawn. Given this pattern and the fact that the predation rate dropped by more than half during the cooler months of the breeding period, the most important predators early in the season might be nocturnal reptiles. The most likely might be the Brown Tree Snake (*Boiga irregularis*), which is common in the area and is active from approximately mid-October to mid-April (Richard Shine pers. comm.). This snake is primarily nocturnal and is a specialized nestling predator (Savidge 1987, Fritts 1988). Some nests were disturbed or had remains of nestlings in or below them. This implies that they were preyed upon by mammals such as rats (*Rattus rattus* or *R. fuscipes*), antechinus (probably *Antechinus stuartii*), or cats (*Felis catus*). Mammals and birds were the most likely nest predators from late April through September. The most common predatory birds were Pied Currawongs (*Strepera graculina*), Gray Butcherbirds (*Cracticus torquatus*), Australian Magpies (*Gymnorhina tibicen*), and Australian Ravens (*Corvus coronoides*), all of which were in the area throughout the breeding period.

Our conclusion that predation was the major cause of nest failure is similar to findings for many other passerines (Ricklefs 1969), although energy shortage has been found to be the major cause of failure in some studies (Clark and Ricklefs 1988). Other studies of breeding in New Holland Honeyeaters have all found that predation was the major cause of nest failure (Paton 1979, Rooke 1979, McFarland 1986), and Bell (1966) noted that predation is a common cause of nest failure in several Australian heathland birds. Bell (1966) noted that the rate of predation

is particularly high in the warmer months of the year (October to March), and that predation by reptiles may limit the ability of heathland birds to breed in late spring and summer. Some species might have breeding periods that avoid the warmer months of the year to avoid seasonal changes in predation rate.

Factors that affect birds' breeding periods include both short-term physiological or behavioral responses to changing conditions and long-term evolutionary responses (Baker 1938, Lack 1954). In some species breeding periods vary from year to year according to environmental conditions. Other species may have fixed breeding periods, either because fixed breeding periods develop early in their lives or because timing of breeding is passed from generation to generation through culture or inheritance. Any effects of predation rates on breeding periods would probably be long-term evolutionary changes, for it would be difficult for birds to assess short-term changes in predation rates.

While energy supplementation indicated that these species did not alter their nesting in response to changes in energy availability in a single year, this does not exclude the possibility that patterns of flowering have had a longer-term role in determining breeding periods or other breeding behaviors. Flowering phenology is fairly consistent on the heath (Pyke 1988, Armstrong 1991a), so fixed breeding periods may be a response to this phenology rather than a response to short-term changes in availability of energy. It is also possible that bird-pollinated plants such as *Banksia ericifolia* (Paton and Turner 1985) could have evolved flowering seasons in response to seasonal changes in bird activity rather than vice versa. Furthermore, the correspondence between breeding and flowering could be completely coincidental.

There is currently more evidence that reproduction is limited by predation than by energy availability, and seasonal patterns in activity of reptile predators are probably just as well correlated with breeding as are seasonal patterns of flowering. More research is needed both to identify the most common nest predators and to determine experimentally whether predation limits reproduction.

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