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Gape Width and Prey Selectivity in the Noisy Friarbird *Philemon corniculatus* and Red Wattlebird *Anthochaera carunculata*

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Optimal foraging theory predicts that predators will select those prey that maximise either energy gain per prey item or per unit foraging time, except when the prey do not satisfy the predator's nutritional requirements (Goss-Custard 1977; Krebs et al. 1977; Avery et al. 1993).

Factors limiting maximum prey size are the gape width of a predator (Zaret 1980; Wheelwright 1985), prey handling time (Recher & Recher 1968; Goss-Custard 1977; Krebs et al. 1977; Sherry & McDade 1982; Avery et al. 1993) and prey defences (Webb &

Shine 1993). The relative importance of each of these factors varies considerably for each predator and its prey. Birds will often spend considerable time bashing prey to improve its palatability; however, swallowing prey whole is a feature of many birds (Lack & Owen 1955, Goss-Custard 1977). Food items are often swallowed whole by frugivorous birds (Wheelwright 1985; White & Stiles 1991; Avery et al. 1993) and insectivorous birds (Lack & Owen 1955). Search time is dependent upon prey availability, and prey handling time by birds is generally determined by prey size rather than

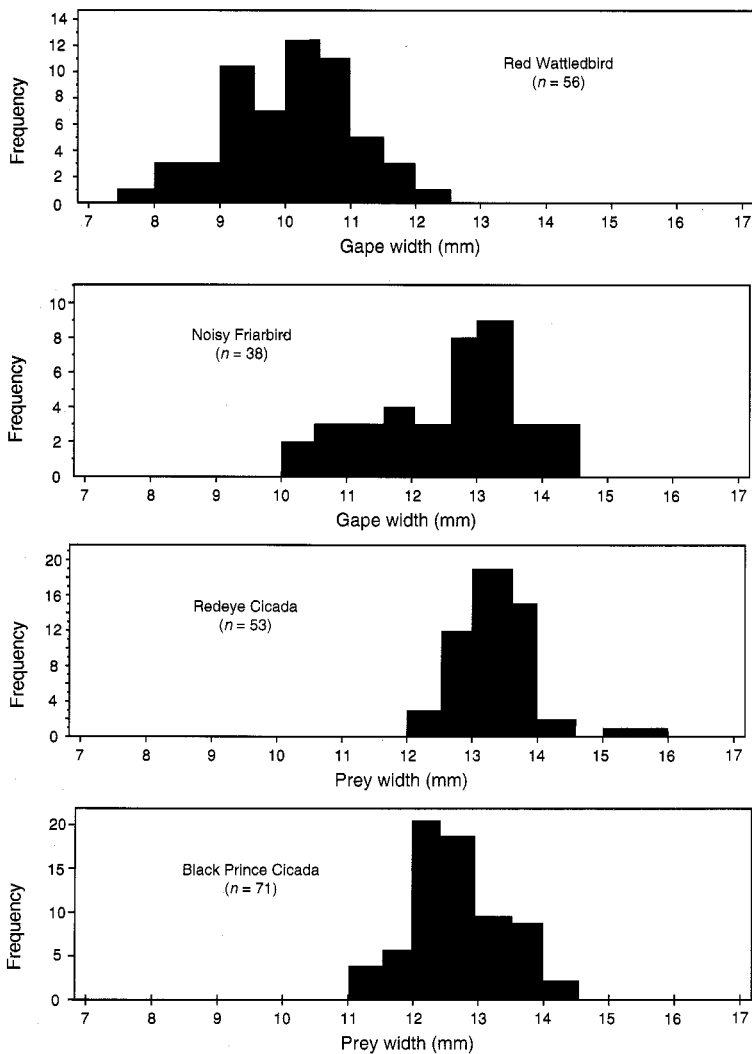


Figure 1 Gape widths of the Red Wattlebird *Anthochaera carunculata* and Noisy Friarbird *Philemon corniculata*. Prey widths of Redeye Cicada *Psaltoda moerens* and Black Prince Cicada *Psaltoda plaga*.

prey defences. The bill of a bird affords a greater advantage over other predatory tools in this respect as prey can be killed at a safer distance from the face. Therefore, the main factor determining maximum prey size in birds is gape width.

The Red Wattlebird *Anthochaera carunculata* and Noisy Friarbird *Philemon corniculatus* are sympatric in south-eastern Australia and occupy similar ecological niches (Blakers et al. 1984; Saunders 1993). Both are generalised feeders, consuming nectar, fruit, seeds, insects and nestlings (Blakers et al. 1984; Longmore 1991). However, there is little published information on

the insectivorous component of their diets. Barker & Vestjens (1990) found cicadas in the diet of both species but Lea & Gray (1936) recorded them only in that of Noisy Friarbirds; neither of these studies identified the cicada species. ASJS has observed Noisy Friarbirds prey upon insects (for example large scarab beetles, cicadas, stick insects and grasshoppers) that are larger than those normally taken by Red Wattlebirds. Nearly all insects were ingested whole and head-first by both species. Redeye Cicadas and Black Prince Cicadas (Hemiptera: Cicadidae) are favourite food items of the Noisy Friarbird during spring/summer. Noisy Friarbirds

will take these cicadas while foraging alongside Red Wattlebirds, which ignore these cicadas.

To determine if the differences in prey preferences were related to gape-limitation, a study of gape widths of both honeyeaters and maximum widths of Redeye and Black Prince Cicadas was undertaken. A detailed description of the foraging strategies of each honeyeater is being prepared for publication elsewhere.

Methods

All New South Wales specimens of the Red Wattlebird and Noisy Friarbird in the collection of The Australian Museum were measured for gape width, while their specimens of the Redeye Cicada and the Black Prince Cicada (Moulds 1990) were measured for prey width. Measurements to the nearest 0.05 mm. were made with vernier calipers. The width of a cicada's head was measured at the widest point when viewed dorsally, i.e. the distance between the outer edges of the eyes. The bill gape width of birds was measured at commissural points of the gape. Comparisons with skulls of these two honeyeaters revealed that the commissural points are very close to the junction of the bill with the skull and that shrinkage is minimal at this point. A more flexible gape in a live bird is still limited by skull dimensions.

There is no evidence of geographical variation in size of these honeyeaters within New South Wales and the nature of their movements within New South Wales is poorly understood (Saunders 1993). The sizes of both cicadas can vary considerably; generally they are larger in wetter seasons, rather than showing geographical variation (M. Moulds pers. comm.). Therefore, data were pooled for each cicada and bird species. Honeyeater adults and juveniles were measured, provided the tail of the juveniles was at least two thirds adult length because juvenile Noisy Friarbirds of this size in the field were observed to be fed whole cicadas.

Data were tested for normality using a Kolmogorov-Smirnov Goodness of Fit and found to be neither normal nor log-normal. Therefore, the Mann-Whitney *U*-test was used to compare the means of the samples (Zar 1984) using STATVIEW STUDENT.

Results

Gape and prey widths are presented in Figure 1. The mean ($\pm$ standard error) gape widths of Red Wattlebirds and Noisy Friarbirds were 10.12 ± 0.13 and 12.56 ± 0.18

mm, respectively. The mean prey width of the Redeye Cicada was 13.35 ± 0.08 mm compared with 12.73 ± 0.08 mm for the Black Prince Cicada. The mean gape width of the Red Wattlebird was significantly smaller than that of the Noisy Friarbird and the mean widths of each cicada species (all $P < 0.001$). The mean gape width of the Noisy Friarbird was also significantly smaller than that of the Redeye Cicada ($P < 0.001$) but not the Black Prince Cicada ($P > 0.05$). However, only two Redeye Cicada specimens (2% of measured specimens) were larger than the maximum Noisy Friarbird gape width.

When the sizes of prey species were combined, only 2% were larger than the maximum gape width of the Noisy Friarbird sample, whereas 68% were larger than the maximum gape width of the Red Wattlebird sample. Nine per cent of gapes of the Noisy Friarbird were too small for any of the sample population of cicadas, whereas 80% of gapes of the Red Wattlebird were too small.

Discussion

Even though there is some sample overlap between prey size and Red Wattlebird gape width they were not observed to forage for these cicadas. This could be because the Red Wattlebirds learn that they are not suitable prey due to their size. They may attempt to ingest large cicadas but quickly learn that they are unable to swallow them. They would therefore soon learn to avoid cicadas because they would be non-profitable prey. This pattern of behaviour has been observed between many predators and potential prey in many birds (Recher & Recher 1968; Sherry & McDade 1982).

In most cases prey handling time and search time appeared to be similar whether the target was small hymenoptera or large cicadas. However, in some cases Noisy Friarbirds were seen to make several attempts to swallow Redeye Cicadas before they were successful, but they were not observed to experience difficulty ingesting Black Prince Cicadas. This suggests that the Redeye Cicada may be approaching the maximum prey size that Noisy Friarbirds can ingest whole. They were not observed to discard large cicadas, although sometimes the insect escaped or out-manoeuvred the pursuing birds during sallies in the warmer part of the day (ASJS unpubl. data).

During seasons when these cicadas are common, other smaller prey items are also abundant and are taken by the Noisy Friarbird. Since search time is much

longer than prey handling time for all insect prey items, it would not be profitable to ignore smaller insects and concentrate only on large prey (Herrera 1978; Thompson 1978; Sherry & McDade 1982; Webb & Shine 1993). However, when feeding dependent young it is more profitable to feed them optimally sized prey because each food packet would contain more energy and nutrients, would incur equal transport costs and would thus promote higher survivorship of the young. Breeding success of Noisy Friarbirds may be closely correlated with cicada density (H.A. Ford pers. comm.). For example, during the drought of the summer of 1993–94 cicadas failed to emerge at Norton's Basin, Wallacia and at The Oaks, Blue Mountains National Park. Noisy Friarbirds did not breed during this period and generally did not remain at these sites, although they had bred there in previous summers. With appropriate rains and the emergence of cicadas in abundance during the summer of 1994–95, Noisy Friarbird densities were much higher and breeding was again recorded at these sites (ASJS unpubl. data).

According to optimal foraging theory, it is most profitable, in terms of energy intake, to take the largest prey items that can be consumed (Lack & Owen 1955; Goss-Custard 1977; Krebs et al. 1977; Zach & Falls 1978; Zaret 1980; Perrins & Birkhead 1983; White & Stiles 1991). When common, the search time for cicadas is not substantially different from that of other prey and since the insects are swallowed whole, handling times are short compared with search time. Although not quantified, observations indicate that search time and prey handling time of cicadas and smaller prey classes are equivalent. Thus, the most likely explanation for differences in prey selectivity between Red Wattlebirds and Noisy Friarbirds is gape width as a limitation on the maximum prey size that can be swallowed.

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