

Temporal variation in food resources determines onset of breeding in an Australian mistletoe specialist

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Abstract. Temporal variation in the onset of breeding has been described for various species in a range of systems. Many of these studies have found a relationship between the timing of breeding and resource levels leading to a matching of life-history stages to resource abundance. However, most of this work has been conducted in northern hemisphere temperate zones – highly regular systems where temperature and other climatic factors have a predictable influence over food abundance. We present data gathered over two years on the timing of breeding in a nomadic mistletoe specialist, the Painted Honeyeater (*Grantiella picta*), relative to temporal variation in the abundance of its main food resource, fruit of the Grey Mistletoe (*Amyema quandang*), in an Australian semi-arid environment. Arrival and departure of the breeding population occurred either side of peak mistletoe fruiting in both years. Clutches were initiated on average on Day 66 of the breeding season (assigned as 1 October for both years) in 2004 (5 December) and Day 49 (18 November) during 2005, i.e. 17 days earlier in 2005. Abundance of mistletoe fruit peaked in January in both years but increased significantly earlier in 2005. Abundance of fruit was almost identical at the mean clutch initiation dates in both years, reaching comparable levels 19 days earlier in 2005. The timing of life-history stages followed the progression of fruiting phenology and was closely matched to resource levels despite marked differences in the temporal availability of fruit between years. Painted Honeyeaters appear similar to northern hemisphere passerines that use photoperiod to time their overall breeding season and then incorporate information from the local environment to fine-tune initiation of breeding. By cuing directly on the food resource, Painted Honeyeaters may avoid temporal mismatching in this highly unpredictable environment.

Additional keywords: frugivory, fruit, *Grantiella picta*, Loranthaceae, matching, Painted Honeyeater, photoperiod.

Introduction

Variation in the abundance of food resources underpins many aspects of the breeding biology of birds. Temporal variation in resources may have substantial influence on the timing of breeding which, in turn, affects reproductive success (Siikamäki 1998; Meijer *et al.* 1999; Nagy and Holmes 2005). If the timing of breeding is mismatched relative to key resource levels, there can be severe consequences for reproductive success (Visser *et al.* 2006). Recent research into the effects of climate change on Great Tits (*Parus major*) has revealed a growing mismatch between breeding and resource levels, leading to increased selection for plasticity in timing of breeding (Nussey *et al.* 2005).

Matching the timing of breeding with fluctuating resource levels may be more critical for dietary specialists. Given their narrow dietary preferences, these specialists may have a more limited ability to vary the timing of breeding outside thresholds set by key nutritional resources. Conversely, dietary generalists may exhibit greater flexibility because they are able to exploit a wider range of resources. As such, the timing of breeding events in resource specialists should closely match the temporal variation in key resource abundance.

Most birds use photoperiod, a temporally fixed abiotic cue, followed by supplemental cues, such as temperature and food

supply, to initiate reproduction (Cockrem 1995; Hahn 1998; O'Brien and Hau 2005). Abiotic or fixed cues may be useful when they predict future changes in resource levels, for example in northern hemisphere temperate zones where spring temperature accurately predicts bud burst and future caterpillar biomass, the principal prey of tits (*Parus* spp.) (Thomas *et al.* 2001; Visser *et al.* 1998, 2006). In environments where the amplitude of variation in resource abundance is high over short time-frames, fixed cues may poorly predict future resource levels and natural selection should favour breeding strategies that uncouple the timing of reproductive events from temporally fixed cues, favouring strategies that depend directly on variation in resource levels.

Many studies have experimentally evaluated the influence of resource variation on the timing of reproduction with the use of supplementary feeding (e.g. Siikamäki 1998; Aparicio and Bonal 2002), most of these studies reporting advances in laying by 2–5 days (Svensson and Nilsson 1995; Nilsson and Kallander 2006). Fewer studies have used designs where data have been collected on the reproductive cycle of a species and on the temporal variation of its food source (Visser *et al.* 2006). Most of these studies were carried out in the northern hemisphere where climate-related proximate cues are generally

predictable (e.g. Svensson and Nilsson 1995; Thomas *et al.* 2001; but see Cockrem 1995; Wikelski *et al.* 2000; Hau 2001).

Although climatic variation is present in northern hemisphere temperate zones, the variability of Australia's climate can be highly irregular, resulting in environments with resources that may be unpredictable in space and time. This offers unique opportunities to test hypotheses about the influence of resource variation on life-history traits. Such a system can enable the uncoupling of the influence of resource variation from fixed cues influencing key life-history stages, thus clarifying relationships between their timing and resource variation and the role of climatic or resource-based cues.

This contribution compares the timing of breeding of a mistletoe specialist, the Painted Honeyeater (*Grantiella picta*), with variation in resource abundance in an Australian semi-arid woodland, relating the timing of laying, hatching and fledging with phenological changes in Grey Mistletoe (*Amyema quandang*). We ask the following questions: (1) When do Painted Honeyeaters arrive in the study area to breed? (2) When do they initiate their clutches? (3) How does the timing of life-history stages relate to mistletoe fruiting phenology? (4) Do Painted Honeyeaters adjust the timing of clutch initiation to match between-year variation in mistletoe fruit abundance? As an extreme dietary specialist, we predict that the Painted Honeyeater will closely match the timing of its breeding activity with variation in fruit abundance.

Methods

Study area

The study was conducted between October 2004 and March 2006 in Binya State Forest, 20 km east of Griffith, New South Wales (NSW), Australia (34°13'S, 140°16'E). The forest has a history of management for timber production, which is reflected in the plant communities currently present. The upper stratum is dominated by White Cypress-pine (*Callitris glaucophylla*) interspersed with Bimble Box (*Eucalyptus populnea*), mallee (*Eucalyptus* spp.), Buloke (*Allocasuarina luehmannii*), Belah (*Casuarina cristata*), corkwood (*Hakea* spp.) and Yarran (*Acacia homalophylla*) which is the main host for Grey Mistletoe at this site. Other species of mistletoe present in the study area (primarily Fleshy Mistletoe (*Amyema mirabilosum*), Box Mistletoe (*Amyema miquelii*) and Needle-Leaf Mistletoe (*Amyema linophyllum*)) occur at low densities and their peak fruiting periods do not coincide with that of Grey Mistletoe. The shrub layer is dominated by saplings of the main canopy species, various acacias (*Acacia* spp.) and hop-bush (*Dodonaea* spp.). African Boxthorn (*Lycium ferocissimum*) is present at low densities. The herbaceous layer is sparse and dominated by annual introduced species, such as Capeweed (*Arctotheca calendula*) and mustards (Brassicaceae) while native chenopods, such as Ruby Saltbush (*Enchylaena tomentosa*) are also common.

The study area experiences hot summers and cool winters with an annual average of 21.3 days with maximum temperatures above 35°C and 19.1 days with minimum temperatures below freezing (BOM 2006). Rainfall is winter/spring dominant (April–October) and highly variable, averaging 406 mm per annum over a 74-year record, with mean monthly rainfall in these months ranging from 32.5 mm to 41.3 mm (BOM 2006).

We obtained climate data from the nearest meteorological station to the study area, the CSIRO Land and Water Laboratory (34°17'S 146°3'E) in the town of Griffith.

Study species

The Painted Honeyeater is an uncommon to rare honeyeater endemic to eastern Australia and found in dry open woodlands containing abundant mistletoes (Higgins *et al.* 2001). It includes some nectar and insects in its diet (Oliver *et al.* 1998) but is considered a dietary specialist, feeding almost exclusively on the fruits of mistletoe in the genus *Amyema* (Higgins *et al.* 2001; Oliver *et al.* 2003). It is known to undertake seasonal north–south movements, considered to be governed principally by the fruiting of mistletoe (Higgins *et al.* 2001).

Arrival and departure of the breeding population

We identified the arrival and departure dates of Painted Honeyeaters in the study area based on a 1-h search conducted weekly at the beginning and end of both nesting seasons during which the presence or absence of Painted Honeyeaters was recorded. Painted Honeyeaters were considered to have arrived in the study area when the first individual was detected and their presence continued to be recorded in subsequent searches. We considered them to have left the study area after three 1-h searches followed by a 12-h search failed to detect a single adult bird.

Breeding season and nest monitoring

We defined Day 1 of the breeding season as October 1 in each year because both Painted Honeyeater sexes were present in the study area in each year during October. Each subsequent day of the nesting season was numbered sequentially until the birds were deemed to have left the study area, thus standardising between-year comparisons. We searched for Painted Honeyeater nests by following individual Painted Honeyeaters and monitoring their behaviour from a distance of approximately 15–20 m with binoculars. We followed the movement path of an individual bird until it either returned to its nest or moved out of view, in which case we attempted to re-establish contact. We monitored the progress of 77 Painted Honeyeater nests every 1–3 days until nest failure (determined by simultaneous disappearance of nest contents), or fledging. For nests that failed we interpolated projected hatching and/or fledging dates using the mean incubation and nestling periods from nests where the clutch initiation and/or hatching dates were explicitly known (L. P. Barea unpubl. data). This enabled a comparison of reproductive chronology with fruiting phenology and fruit abundance indices between years. The analysis is based solely on first clutches of the season, defined as the day the first egg appeared in a nest (after Arnold *et al.* 2006; Nager and van Noordwijk 1995).

Fruit abundance

Abundance of Grey Mistletoe fruit within the study area was measured over two seasons (between October 2004 and April 2006), with monthly counts of ripe fruit on a tagged branch of 24 randomly selected mistletoe plants along three 240-m transects ($n = 72$ mistletoes) in a manner modified from López-de Buen and Ornelas (2001). Transects were located within Painted Honeyeater nesting habitat, corresponding to areas of high

mistletoe density. An overall index of fruit abundance was calculated – expressed as the number of ripe fruits per 0.3 m of branch, measured proximally from the tip of the branch and averaged across each transect – to reflect abundance of fruit in the general study area. To ensure independence of the seasonal samples, we selected new mistletoe plants along the same transects in October 2005.

Data handling and statistical analysis

All statistical analyses were performed in SPSS Version 14.0 (SPSS 2006). Once visual inspection of residual plots from linear regression models approximated a normal distribution, we used linear regression to model the timing of life-history stages against estimated resource levels, using the regression equations for the monthly fruit-abundance indices during the period fruit abundance increased in each year. We used Mann–Whitney U tests for between-year comparisons of reproductive and resource abundance metrics and considered results to be statistically significant when P values were <0.05 .

Results

Fruit abundance

Abundance of fruit differed between transects but followed similar phenological patterns (Fig. 1). Because each transect showed a similar trend and it was the temporal variation in fruit abundance that was of prime interest, we used the average value across all three transects for each month to represent overall fruit abundance across the study area. Fruit was available in all months of the year but abundance followed a unimodal seasonal pattern characterised by an extended period of scarcity from late summer through winter (wet season) followed by a peak in abundance during the dry summer (Fig. 1).

Fruit abundance increased linearly between October and January in both years (2004 $R^2 = 0.91$, $y = 0.0142x - 0.4178$; 2005 $R^2 = 0.93$, $y = 0.0121x - 0.0516$) but was significantly

Table 1. A comparison of fruit-abundance indices of Grey Mistletoe ($n = 72$ plants) during the 2004 and 2005 peak fruiting periods at Binya State Forest, NSW, Australia

During 2005, fruit-abundance indices were significantly higher before the peak in fruit abundance than during 2004. The indices were significantly lower during February and March in 2005 consistent with the temporal shift in fruit abundance

Month	Fruit index – 2004 (s.e.)	Fruit index – 2005 (s.e.)	U	P
October	0.04 (0.04)	0.12 (0.10)	2340	0.03
November	0.07 (0.02)	0.66 (0.50)	1641	<0.001
December	0.84 (0.30)	1.10 (0.40)	2415	0.47
January	1.23 (0.22)	1.22 (0.40)	2570	0.93
February	1.19 (0.40)	0.18 (0.10)	1156	<0.001
March	0.65 (0.13)	0.06 (0.00)	1458	<0.001

more abundant during October and November in 2005 (i.e. earlier) than during the same period in 2004 (Table 1). Although mistletoe fruit was more abundant in December 2005 than in December 2004, the difference was not significant. In both seasons, abundance of fruit was highest during January when the indices were almost identical and the median index values were not significantly different (Fig. 2). The peak in abundance of fruit in both years represents an almost 25-fold increase in the abundance index over the winter low period.

After the January peak, abundance of fruit decreased (Fig. 1), declining significantly earlier and more rapidly in 2005 than during the 2004 season (mean February fruit abundance indices 0.18 ± 0.10 s.e. for 2005 and 1.19 ± 0.40 for 2004, Mann–Whitney $U = 1156$, $P < 0.001$, $n = 144$, Table 1). When considered over the whole peak fruiting period, the data show similar phenological patterns in each year, but a temporal shift in the 2005 season resulted in an earlier increase and earlier decline in fruit abundance (~20 days) for that year.

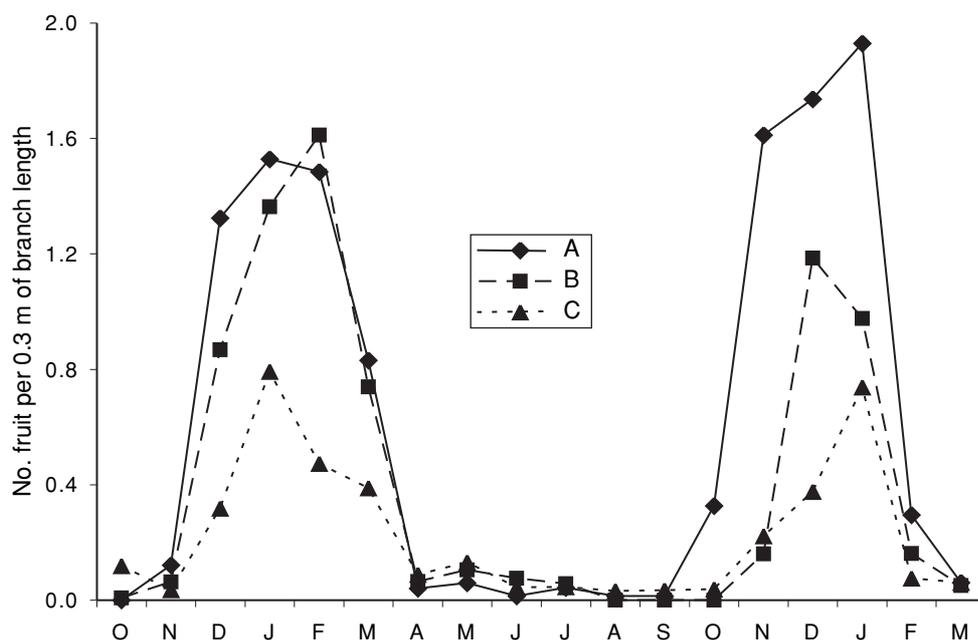


Fig. 1. Temporal variation of abundance of Grey Mistletoe fruit between October 2004 and March 2006 in Binya State Forest, NSW, Australia, showing similar overall phenology pattern across the three transects (A, B, C).

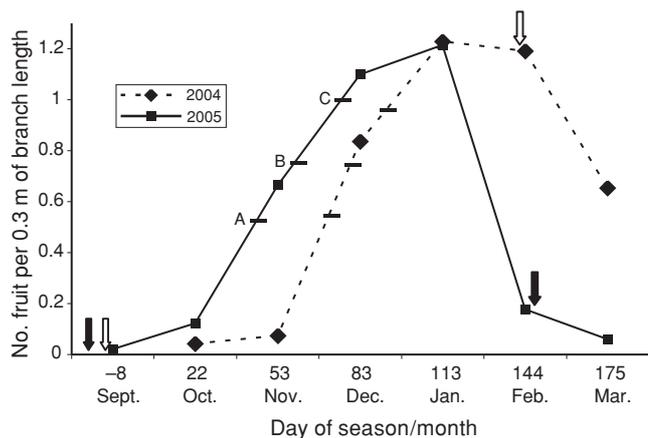


Fig. 2. Variation in fruit abundance indices during the 2004 and 2005 Painted Honeyeater breeding seasons showing the temporal shift in resource abundance, arrival and departure of the population (open arrows – 2004, black arrows – 2005), and the timing of life-history stages in relation to resource levels (mean and standard errors are shown in Table 2). Horizontal axis expresses time as day of season and month. 1 October is Day 1 of the breeding season in both years. A = mean clutch initiation date, B = mean hatching date, C = mean fledging date (dates correspond to interpolated mean resource levels, calculated using linear regression, see Table 2).

Rainfall and temperature

In both calendar years, rainfall varied greatly (monthly totals ranged from 0.4 mm to 44.4 mm and 2.6 mm to 70.2 mm for 2004 and 2005 respectively), being lowest during summer–autumn and highest during the winter–spring period. During the 5 months preceding the increase in fruit abundance (i.e. during fruit development), substantially more rainfall was recorded in 2005 (264.6 mm) than during the same period in 2004 (103.8 mm). The total rainfall for the months of September and October combined (i.e. when Painted Honeyeaters were present in the study area) was also higher in the 2005 season (total of 108 mm and 25 mm for 2005 and 2004 respectively).

Mean daily temperatures during September and October were similar in both years ($14.7^{\circ}\text{C} \pm 0.56$ s.e. and $13.70^{\circ}\text{C} \pm 0.45$ s.e. for 2004 and 2005 respectively) and the median

values (14.50°C and 13.40°C for 2004 and 2005 respectively) did not differ significantly (Mann–Whitney $U = 1696$, $P = 0.40$, $n = 122$ days).

Timing of reproduction in relation to annual variation in resources

Over the course of the 2004 and 2005 breeding seasons we located 77 nesting attempts by Painted Honeyeaters ($n = 34$ in 2004, $n = 43$ in 2005) that resulted in a clutch being initiated. We did not include in the analysis nests that were known or suspected to be re-nesting attempts after previous nesting failure or success. Therefore, this analysis is based on 51 nests for which initiation dates of clutches were either explicitly known or calculated from observed hatching or fledging dates using the median value for incubation or nestling periods (16 days and 17 days respectively; L. P. Barea, unpubl. data). Nine nests located during the 2004 nesting season and included in this analysis were found outside Binya State Forest either in remnant vegetation along the Whitton Stock Route adjacent to Binya State Forest ($n = 4$) or in similar habitat within 10 km of the study area ($n = 5$). With the exception of a single nest in the Whitton Stock Route during the 2005 season, all of the nesting attempts were located within Binya State Forest.

Arrival and departure of the breeding population

Male Painted Honeyeaters arrived about 3 weeks before females (i.e. by 10 and 4 September in 2004 and 2005 respectively) and the breeding population left the study area before 12 February 2005 in the 2004 season, and before 20 February 2006 in the 2005 season. Both sexes appeared to leave simultaneously.

Initiation of clutches

Table 2 shows the mean time of occurrence for the reproductive parameters studied and the associated fruit-abundance indices for both seasons. The mean date of initiation of clutches for all clutches in 2004 was Day 66 (5 December) of the nesting season. Clutches were initiated on average 17 days earlier during 2005 (mean 18 November, Day 49) and the differences were significant (Table 2). Although clutches were initiated significantly earlier during the 2005 season, the median dates of clutch initiation in each season corresponded to the initial increase in fruit abundance in both years, and were almost iden-

Table 2. Reproductive parameters and fruit-abundance indices for two Painted Honeyeater nesting seasons at Binya State Forest, NSW, Australia

Mann–Whitney statistics are not provided for hatching and fledging dates because they are not independent of dates of initiation of clutches. FAI-CI = fruit abundance index at mean clutch initiation date; FAI-PH = fruit abundance index at mean hatching date; FAI-PF = fruit abundance index at mean fledging date. Days of season are rounded to nearest whole day. n = number of nests

Parameter	2004	n	2005	n	U	P	n
	Mean (s.e.)		Mean (s.e.)				
Clutch initiation (day of season)	66 (2.05)	21	49 (2.90)	30	120	<0.001	51
Hatching (day of season)	81 (2.05)	21	65 (2.90)	30	–	–	–
Fledging (day of season)	99 (2.05)	21	81 (2.90)	30	–	–	–
FAI-CI	0.51 (0.03)	21	0.54 (0.04)	30	287	0.60	51
FAI-PH	0.74 (0.03)	21	0.73 (0.04)	30	301	0.79	51
FAI-PF	0.98 (0.03)	21	0.93 (0.04)	30	260	0.29	51

tical (Fig. 2; Table 2). The mean fruit-abundance indices were almost identical at this time (Fig. 2), reaching equivalence 18.90 days earlier during 2005.

Hatching

Mean date of hatching in 2004 and 2005 corresponded to Days 81 and 65 respectively, coinciding with the middle of the period of rapid increase in fruit abundance. The mean fruit-abundance indices were almost identical at this time (Fig. 2), but reached equivalence 16.20 days earlier during 2005, and showed no significant difference in their median values at the time of mean hatching in either season (Table 2).

Fledging

In both years, the mean date of fledging corresponded with Days 99 and 81 for 2004 and 2005 respectively, coinciding with fruit abundance just before its peak and rapid decline (Fig. 2). The mean fruit-abundance indices were nearly identical and reached equivalence 13.23 days earlier during 2005. Their median values were not significantly different from each other at the mean time of fledging (Table 2).

Discussion

Painted Honeyeaters timed the onset of their breeding to match closely the abundance of mistletoe fruit despite temporal differences (see Fig. 2). In this study, the fruiting phenology of Grey Mistletoe appeared seasonal on an annual scale but the overall peak in fruit abundance differed by ~20 days between years. After their arrival in the study area, Painted Honeyeaters responded to supplementary cues so that the sequence of nesting events closely matched the phenology of Grey Mistletoe, despite a temporal shift in fruit abundance early in the season. Resource levels at the mean time for each life-history stage were the same in both years, reflecting a close matching of reproductive effort with resource levels (see Fig. 2). The timing of first clutches in both years resulted in the nestling and fledging periods coinciding with increasing fruit abundance so that on average nestlings fledged just before the peak in fruit resources, that is the time of highest resource needs coincided closely with time of highest resource availability.

This finding differs from the food supplementation study of Armstrong and Pyke (1991), who found that although the seasonal patterns of reproduction in New Holland Honeyeaters (*Phylidonyris novaehollandiae*) and White-cheeked Honeyeaters (*P. nigra*) were related to periods of high nectar availability, the birds did not make fine-scale adjustments when nectar availability was experimentally increased early in the season. It is worth noting, however, that some northern hemisphere birds have been observed to initiate clutches earlier when their food resources have been artificially increased (e.g. Svensson and Nilsson 1995; Kelly and Van Horne 1997).

If the timing of initiation of clutches in 2005 had been the same as that of 2004, the Painted Honeyeater's reproductive chronology would have been mismatched relative to the peak of fruiting, with fruit abundance rapidly declining shortly after the nestlings fledged. This would presumably have resulted in reduced fitness given that a relationship between the matching of breeding with resource peaks and reproductive success has been shown for other species (e.g. Siikamäki 1998; Verhulst and

Tinbergen 2001). Such a scenario would also have reduced the opportunity for successful completion of second clutches.

Photoperiod may act as the initial cue driving the arrival of Painted Honeyeaters on their breeding grounds, as is the case for most temperate zone birds (O'Brien and Hau 2005). The arrival and departure dates were similar in both years and they arrived before the increase in fruit abundance and departed as it was rapidly declining. This is not surprising, given that the birds cannot 'read' local environmental cues before their arrival. Once they have arrived, they appear to use short-term supplementary cues to modulate the fine-scale timing of reproductive activity.

Our analyses indicate that Painted Honeyeaters timed their departure from the study area in response to the rapid decline in fruit abundance and suggest that breeding is limited by predictable food shortages, as has been suggested for other frugivorous birds (Worthington 1982). The influence of temporal variability in food abundance has been implicated in the timing of breeding for other honeyeaters, e.g. Silver-crowned Friarbirds (*Philemon argenteiceps*; Noske and Franklin 1999), Noisy Friarbirds (*P. corniculatus*; Tokue and Ford 2006) and New Holland Honeyeaters (Ford 1980; Paton 1982). However, the patterns of timing of breeding in Meliphagidae vary greatly and appear to be the product of current ecological processes rather than phylogenetic history (Tokue and Ford 2006) and this also appears to be the case for the Painted Honeyeater. At this stage, the relative importance of photorefractoriness and declining resources in determining the cessation of breeding activity is unclear and requires further exploration.

What drives initiation of clutches?

Mean daily temperatures during the period directly preceding initiation of clutches and subsequent life-history stages were not significantly different between years. In contrast with some northern hemisphere systems (Perrins and McCleery 1989; Dunn and Winkler 1999; Meijer *et al.* 1999; Nussey *et al.* 2005; Nilsson and Kallander 2006), this suggests that temperature lacked precision as a predictor of future resource levels and, as such, the birds cue on some other factor or factors to initiate breeding.

Total rainfall over the same period and for the 5 months preceding the peak in fruit abundance was significantly greater in 2005 than 2004. Although increased rainfall in the months preceding the 2005 season may have contributed to the temporal shift in fruiting phenology, it is unlikely that Painted Honeyeaters used rainfall as a direct cue. This is because they arrived in the study area shortly before initiating their first clutches (~30 days after females arrived). Moreover, the first fruits of the 2005 season ripened over a period of 6 months (L. P. Barea, unpubl. data) and their developmental rate would presumably be influenced by rain falling long before the Painted Honeyeaters were present in the study area. Finally, given the indirect influence of rainfall on parasitic plants (water relations buffered by the host), phenological patterns of mistletoes are less sensitive to climatic variability, reflecting instead a range of host-mediated factors (Ehleringer 1989; Ehleringer and Marshall 1995; Bowie and Ward 2004). In sum, rainfall in the period preceding nesting is unlikely to have had a direct effect on initiation of clutches in Painted Honeyeaters, and cannot account directly for the observed level of resource matching.

Within the window defined by photoperiod, Painted Honeyeaters could cue directly on the phenological development of fruit by tracking the rate at which it ripens. Before the increase in fruit abundance each year, Painted Honeyeaters spent much of their time foraging in mistletoe plants feeding primarily on mistletoe nectar, and were frequently observed manipulating unripe fruit in their mandibles followed by either eating the still green fruit (fruits are pale yellow when ripe) or rejecting it. Oliver *et al.* (2003) also observed this behaviour in Painted Honeyeaters in northern NSW in October 2001 before Grey Mistletoe fruit had ripened – at that time Grey Mistletoe nectar was the dominant food resource.

The potential for direct food-based tactile cues influencing the timing of breeding has been shown experimentally for Spotted Antbirds (*Hylophylax naevioides*), suggesting that food cues alone can initiate gonadal development (O'Brien and Hau 2005). Cockrem (2006) suggested a similar mechanism involving visual and tactile cues from a range of foods was involved in the timing of breeding in Kakapo (*Strigops habroptilus*). Evidence for the use of food as a specific proximate cue in timing of breeding has also been shown for Piñon Jays (*Gymnorhinus cyanocephalus*; Ligon 1978) and Red Crossbills (*Loxia curvirostra* complex; Hahn 1995). Manipulation of unripe fruits or the increasing presence of pale-yellow ripe fruits early in the breeding season, or both, could provide a mechanism by which Painted Honeyeaters are able to track changes in abundance of ripe fruit, predict future resource levels and time their breeding activity accordingly.

The degree of resource matching with life-history stages may be especially pronounced in this species because it is a dietary specialist, with opportunities for breeding constrained in space and time by the abundance of mistletoe fruit. Generalists would presumably exhibit reduced levels of resource matching and a greater amplitude in the timing of major life-history events than specialists. For example, the generalist Regent Honeyeater (*Xanthomyza phrygia*) showed significant variability in resource selection, hence reduced resource matching, between breeding seasons (Oliver 2000). Further research encompassing species exhibiting a range of dietary strategies coupled with fine-grained measurements of changing resource levels should shed light on the role of temporally variable resources on the timing of reproduction by dietary specialists and generalists alike. However, the difficulty of collecting fine-grained resource information for generalists and functional responses such as resource-switching, opportunism and regional differences in resource-use complicate such work. Notwithstanding these challenges, the honeyeater family includes many species exhibiting a range of dietary strategies from extreme specialists, such as the Painted Honeyeater, to insectivores and facultative frugivore-nectarivores that offers potential for such research.

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