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THE DIET OF THE NORTH ISLAND KAKA (*NESTOR MERIDIONALIS SEPTENTRIONALIS*) ON KAPITI ISLAND

Summary: Food of the North Island kaka (*Nestor meridionalis septentrionalis)* on Kapiti Island was identified while quantifying the foraging activity of nine radio-tagged birds from March 1991 to January 1992. Additional food types were identified by opportunistic observation of feeding birds and qualitative examination of nestling faeces. A diverse range of food was taken, including wood-boring invertebrates, scale insects, seeds, nectar or pollen, fruits, and sap. Radio-tagged birds foraged predominantly for invertebrates over most of the year, but hinau (*Elaeocarpus dentatus*) seed, five-finger (*Pseudopanax arboreus*) nectar or pollen and tawa (*Beilschmiedia tawa*) seed were seasonally important food types. Most of the plant food taken by kaka on Kapiti is known to be eaten, or otherwise reduced in abundance, by Australian brushtail possums (*Trichosurus vulpecula*), a widespread potential competitor that has been eradicated from Kapiti. Annual variation in the abundance of important plant food types may explain variation in the breeding intensity of kaka on Kapiti Island.

Keywords: Kaka, *Nestor meridionalis*, diet, foraging behaviour, phenology, competition, seed predation, frugivory, insectivory.

Introduction

The North Island kaka (*Nestor meridionalis septentrionalis;* nestorinae) is a large (358-555 g, n = 39 [Moorhouse *et al., in press*]) forest-dwelling parrot endemic to New Zealand (Oliver, 1974; Heather and Robertson, 1996). Formerly widespread on all three main islands and their forested offshore outliers (Potts, 1882; Buller, 1888; Oliver, 1974), the range of the kaka has contracted rapidly since European colonisation (Oliver, 1974; Bull, Gaze and Robertson, 1985). While deforestation has destroyed or degraded much of the kaka's original habitat (Oliver, 1974), the fact that the bird has become rare even within unlogged native forest remnants (Bull *et al.,* 1985; C. F. J. O'Donnell *pers. comm.*) suggests that introduced predators and competitors have also been important factors in its decline.

Research by Wilson *et al*. (*in press*) suggests that predation of nesting females by introduced stoats (*Mustela erminea*) poses the greatest immediate threat to kaka. In one population, stoats were found to have killed four of the five females known to be nesting in a single breeding season (Wilson *et al., in press*). Although considerably more difficult to quantify, competition for food with introduced species, such as the Australian brushtail possum (*Trichosurus vulpecula*), wasps (*Vespula*

spp.), and rats (*Rattus* spp.), may also be contributing to the decline of kaka by reducing the birds' productivity (Beggs and Wilson, 1991). A significant competitive interaction with possums is suggested by the fact that kaka remain common in the South Island only where possum densities are relatively low (O'Donnell and Dilks, 1986).

Supplementary feeding has not increased the low nesting frequency of a South Island kaka (*N. m. meridionalis*) population (Wilson *et al., in press*). This suggests that low productivity was not a consequence of competition for food with introduced species. Breeding in this population appears to depend on the availability of red beech (*N. fusca*) seed, a periodically superabundant food which is not limited by introduced species (Wilson *et al., in press*). However, as kaka have a diverse diet (O'Donnell and Dilks, 1994) and occur in a wide range of forest types (Oliver, 1974), competition with introduced species for food could be significant elsewhere.

Supplementary feeding experiments can provide only limited evidence for or against competition. If supplementary feeding fails to increase productivity it is possible that insufficient food was provided to compensate for that consumed by competitors. Conversely, if supplementary feeding increases productivity, it does not follow that the population

concerned would necessarily have the same level of nutrition, and productivity, in the absence of competitors.

More reliable evidence for a significant competitive interaction between two species is a significant increase in the productivity of the inferior competitive species following the eradication, or sustained control, of the superior competitor. Unfortunately, although possums have been eradicated from two offshore islands which have kaka (Codfish I. and Kapiti I.), the productivity of the birds was not quantified prior to either eradication. Quantitative estimates of kaka productivity in the presence of two rat species are available for the Kapiti population (Moorhouse, 1991) but their productivity in the absence of rats remains unknown.

Introduced herbivores change forest composition (Kean and Pracy, 1953; Fitzgerald, 1976; Coleman, Gillman and Green, 1980; Brockie, 1992) and reduce or entirely eliminate food crops formerly available to native birds (Leathwick, Hay and Fitzgerald, 1983; Fitzgerald, 1984; Wilson, 1984; Cowan, 1991; Cowan and Waddington, 1990; Brockie, 1992). Consequently, it is important to evaluate the potential for competition between such species and kaka.

The first step in assessing the potential for food competition between kaka and introduced species is to obtain information on the diet of the bird in a range of habitat types. Since introduced herbivores can alter the range of plant foods available to native birds, it is informative to compare the diet of kaka in the presence and absence of suspected competitors. Two potential competitors, wasps and rats are now virtually ubiquitous throughout the kaka's remaining range. However, information on kaka diet in the absence of possums, another widespread potential competitor (O'Donnell and Dilks, 1986; Beggs and Wilson, 1991), can be obtained from several offshore island populations where possums are absent.

Another reason for investigating kaka diet is to clarify the relationship between breeding intensity and food abundance. In the population studied by Beggs and Wilson (1991) nesting has been recorded in only six out of eleven years, in each case coinciding with the seeding of red beech (Wilson *et al., in press*). Although the apparent dependence of this population on a single periodically superabundant food source could reflect the relatively limited range of foods available to birds in beech forest (Wardle, 1984), kaka also display considerable annual variation in the incidence of nesting on Kapiti Island (Moorhouse, 1991), a habitat of considerably greater floristic diversity (Esler, 1967).

Similar restriction of nesting to years in which a specific plant food is unusually abundant also occurs in two other endemic parrots, the kakapo (*Strigops habroptilus*) (Powlesland *et al.*, 1992) and the yellow-crowned parakeet (*Cyanoramphus auriceps*) (Elliott *et al.* 1996). In all three species, the food associated with increased nesting activity are not eaten until after laying and are provided to nestlings and fledglings (Powlesland *et al.*, 1992; P. R. Wilson *et al., in press*). Although food appears to be generally limited for most birds during the nestling-fledgling period (Martin, 1987) it is unusual for altricial species (other than raptors) not to attempt to breed due to insufficient food resources (*op. cit.*).

If the breeding intensity of kaka is determined by food abundance during the nestling-fledgling period, identification of the specific food that influences nesting in different habitats has considerable benefits for management. If potentially important plant species are significantly reduced by introduced herbivores, control of the latter could improve the productivity of kaka. Identification of important plant food may also allow prediction of the years in which breeding attempts are most likely to occur. Only nesting females (Beggs and Wilson, 1991), nestlings (Moorhouse, 1991) and young fledglings (Moorhouse and Greene, 1995) appear to be vulnerable to introduced predators. The ability to concentrate predator control in the years in which most breeding attempts occur would greatly improve cost-effectiveness.

Present knowledge of the diet is confined to studies of the South Island sub-species in beech forest (Beggs and Wilson, 1991) and broad-leaved forest (O'Donnell and Dilks, 1994). In this paper I describe the diet of the North Island kaka (*N. m. septentrionalis*) in the seral mixed hardwood forests of Kapiti Island, discuss the implications of dietary overlap between kaka and possums and the relationship between food abundance and breeding intensity.

Study area

Kapiti Island (1965 ha; 40°, 51' S, 174°, 55' E; maximum elevation 521 m) is a nature reserve administered by the New Zealand Department of Conservation. Apart from Norway (*R. norvegicus*) and Polynesian rats (*R. exulans*), the island has been free from introduced mammals since the eradication of possums between 1981 and 1986 (Cowan, 1992a). Introduced wasps are present but do not (*pers. obs.*) reach the densities recorded in beech forest habitats of the kaka (Sandlant and Moller, 1989).

The predominant vegetation cover of Kapiti Island (81%) is a diverse mosaic of indigenous seral forest and shrubland (Esler, 1967). Common tree species include five-finger (*Pseudopanax arboreus*), kanuka (*Kunzea ericoides*), kohekohe (*Dysoxylum spectabile*) and tawa (*Beilschmiedia tawa*). Common co-dominants include hinau (*Elaeocarpus dentatus*), karaka (*Corynocarpus laevigatus*) and mahoe (*Melicytis ramiflorus*). Northern rata (*Metrosideros robusta*) and pukatea (*Laurelia novae-zelandiae*) occur as scattered emergents (Esler, 1967).

Methods

Diet

The foraging activity of nine radio-tagged kaka (three males: two adults, one sub-adult, and six females: two adults, four of indeterminate age) was quantified between March 1991 and January 1992. These birds were sexed on the basis of culmen length (Moorhouse *et al*. *in press*), and fitted with two-stage radio-transmitters prior to release. Age was assessed according to the criteria described by Moorhouse and Greene (1995). In addition to systematic observations of the foraging behaviour of these birds, opportunistic observations of kaka feeding behaviour were made between 1988 and 1991 and seeds found in nestlings' faeces were identified. Although supplementary food (cheese and sugar-water) was provided daily to kaka on Kapiti, only one radio-tagged bird was observed taking this food.

Foraging activity was observed from 0900 to 1700 hours New Zealand standard time on the assumption that this period was representative of daily foraging activity. As kaka were active after dark on Kapiti, it was not possible to observe their complete daily activity cycle. Due to their high mobility, it was not always possible to locate or observe all radio-tagged birds each month. A maximum of seven and a minimum of four radio-tagged kaka were observed monthly between March 1991 and January 1992, except December when no data were collected.

Once sighted, an individual bird's behaviour was recorded at one minute intervals in accordance with an instantaneous behavioural sampling regime (Martin and Bateson, 1993) until a target of 100 foraging observations had been obtained each month. This goal was usually achieved (mean number of foraging observations per bird per month ± 95% confidence limits = 97 ± 3, n = 56). The number of days required to obtain the target 100 foraging observations varied from one to three, but one was usually sufficient (37 of the 53 completed samples [70%] were obtained in a single day). The maximum time interval over which a single sample was collected was nine days.

Foraging activity was categorised according to the food item being taken. All plant foods were identified to the species level. With the exception of scale insects, it was not possible to identify the invertebrate component of the diet to species and this was therefore treated as a single food category - wood or bark dwelling invertebrates (hereafter WBI). Behaviour other than foraging was categorised as: sleep, preening, sitting (at rest) and social behaviour, the latter encompassing all forms of social interaction with other individuals, including vocalisation.

Plant phenology

A phenology transect comprising from 10 to 44 individually marked trees of 27 species was established on Kapiti Island in June 1989. The species monitored were either known kaka food plants or common species which produced fruits or nectar palatable to other birds. One common species, pukatea, was not monitored because it nearly always occurs as a tall emergent on Kapiti and it was difficult to observe its flowers and fruits. Introduced species of limited distribution were omitted, even if known to provide food for kaka, because these food sources were not available to the majority of birds on the island.

As dioecious trees could only be sexed by floral anatomy or the presence or absence of fruit, this would have introduced a sampling bias toward individual trees that were actually producing flowers or fruit. For this reason I chose individual trees solely on the basis of how easily I could observe their canopy for flower or fruit formation. As the same individuals were monitored throughout the study, only a gross bias in the sex ratio would affect relative indices of flower or fruit abundance between years.

The phenology transect was monitored monthly from June to September 1989, January to May 1990 and from January 1991 to January 1992. The abundance of flowers and fruit on individual trees was recorded on a scale of one to four (one = zero, two = ones to tens, three = hundreds, four = thousands).

Breeding season and breeding intensity

The timing of kaka breeding activity and its intensity was assessed by inspecting known nest sites (Moorhouse, 1990).

Results

Diet

A diverse range of plant food (Table 1) and invertebrates (Table 2) was eaten by kaka on Kapiti Island. Most of the plant foods eaten by kaka on Kapiti are known to be eaten by possums (Table 1). The absence of any obvious relationship between the number of food types radio-tagged birds were observed eating and the length of the time interval within which foraging observations were collected (Figure 1) suggests that the results were unbiased with respect to variation in time required to obtain the monthly target of 100 foraging observations. All radio-tagged birds spent the greater proportion of time foraging when under observation (Figure 2A). Sleep was the next most frequent activity in all but one bird, followed by preening and sitting at rest (Figure 2A). As the most atypical bird (Bird 7) was the one for which the least data were obtained (Figure 2A), its apparent aberrance could reflect sampling error rather than individual variation. Social behaviour was observed in only three individuals and in each case was less than 5% of their observed diurnal activity (Figure 2A). All but one radio-tagged birds (Bird 2) foraged predominantly for WBI (Figure 2B). As Bird 2 was the only radio-tagged bird which took supplementary
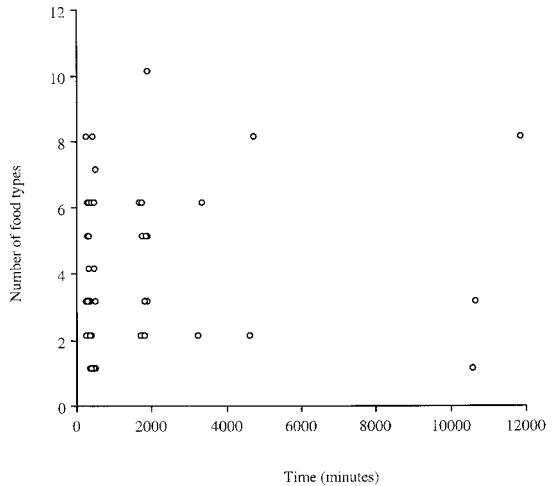

Figure 1: *Relationship between number of different foods radio-tagged kaka on Kapiti Island were observed taking and the time interval within which 100 instantaneous foraging observations were collected (n = 53).*

food, its foraging behaviour may have been atypical. Seeds were the next most frequently taken food, followed by nectar, fruit, sap and scale insects (Figure 2B).

The proportion of time birds spent foraging relative to other activities varied considerably from

Table 1: *Plant foods of North Island kaka on Kapiti Island. Y = eaten by kaka, - = not observed eaten, * = eaten by most radio-tagged birds (see methods for explanation),* [†] *= eaten by possums (indicates consumption of flowers and flower buds in the case of nectar/pollen sources), X = locally extinct or rare, P = seed production suppressed.*

Plant species	Seed	Fruit	Nectar/Pollen	Possum effect
five-finger (*Pseudopanax arboreus*)	-	Y[†]	Y*	X
hinau (*Elaeocarpus dentatus*)	Y*	Y*[†]	Y[†]	P
karaka (*Corynocarpus laevigatus*)	Y	Y[†]	-	
karo (*Pittosporum crassifolium*)	-	Y	Y	
kawakawa (*Macropiper excelsum*)	-	Y[†]	-[†]	
kanuka (*Kunzea ericoides*)	-	-	-	
kiekie (*Freycinetia banksii*)	-	Y[†]	Y[†]	
kohekohe (*Dysoxylum spectabile*)	Y	-[†]	Y	
kohuhu (*Pittosporum tenuifolium*)	-	Y[†]	-	
lancewood (*Pseudopanax crassifolium*)	-	Y[†]	-	
mahoe (*Melicytus ramiflorus*)	-	-	Y	
matai (*Prumnopitys taxifolia*)	-	Y[†]	-	
northern rata (*Metrosideros robusta*)	-	-	Y[†]	X
pigeonwood (*Hedycarya arborea*)	-	Y[†]	-	
pohutukawa (*Metrosideros excelsa*)	-	-	Y	
pukatea (*Laurelia novae-zelandiae*)	Y	-	-	
putaputaweta (*Carpodetus serratus*)	-	-	-	
rewarewa (*Knightia excelsa*)	-	-	Y[†]	
tawa (*Beilschmiedia tawa*)	Y*[†]	Y*[†]	-	P
wharangi (*Melicope ternata*)	Y	-	-	

References: Kean and Pracy (1953), Mason (1958), Fitzgerald (1976), Fitzgerald and Wardle (1979), Meads (1976), Coleman *et al*. (1980), Cowan (1990, 1992b), Cowan and Waddington (1991), Brockie (1992).
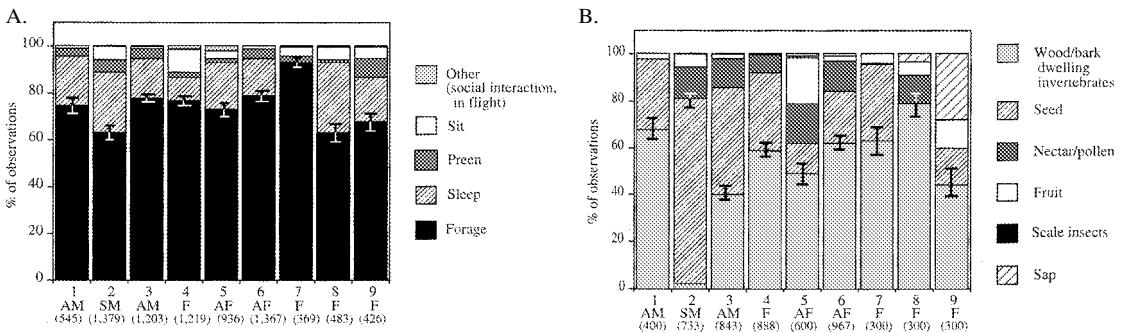
Figure 2: *Breakdown of (A) general activity budget and (B) foraging activity of radio-tagged North Island kaka on Kapiti Island between March 1991 and January 1992. Values shown are proportions of observed activity in each behaviour or foraging category and the maximum 95% confidence limits. Numbers identify individual birds; those in parentheses indicate the number of observations per bird. Letters indicate age and sex; A = adult, S = sub-adult, M = male, F = female.*

Table 2: *Invertebrates eaten by North Island kaka on Kapiti Island.*

1. Small (< 1-2 cm long) coleopteran or lepidopteran larvae extracted from dead branches of hinau, karaka, and tawa.
2. Large (c. 3-5 cm long) coleopteran or lepidopteran larvae extracted from live wood of kanuka and putaputaweta (*Carpodetus serratus*). Probably those of the kanuka longhorn beetle (*Ochrocydus huttonii*) and the puriri moth (*Charagia virescens*).
3. Larvae of an undescribed gall midge (Cecidomyiidae: Diptera) extracted from putaputaweta galls.
4. The six-penny scale insect (*Ctenochiton viridis*) gleaned from five-finger and tawa leaves.
5. Unidentified invertebrates, possibly including tree-weta (*Hemideina* spp.) nymphs, extracted from dead twigs of five-finger, mahoe, hinau, northern rata, kohekohe and pigeonwood.

month to month, increasing from March to June, and from September to November (Figure 3A). Marked seasonal variation in diet was also apparent. Although most birds foraged primarily for WBI over most of the year (Figure 3B), all birds located in March were feeding primarily, and in most cases exclusively, on hinau seed (Figure 3C). This included Bird 4, which was the only radio-tagged bird feeding young at this time (Figure 3C).

Although two males continued to feed primarily on hinau seed until June, all females stopped eating it after March (Figure 3C). Bird 4, the bird with a dependent fledgling, foraged exclusively for pukatea seed in April (Figure 3D), while the two non-breeding females located that month foraged either exclusively (Bird 6), or predominantly (Bird 5) for WBI (Figure 3B). Bird 4 was not observed foraging

for WBI until June (Figure 3B), by which time her single fledgling was largely independent. Most birds spent > 30% of their observed foraging activity feeding on five-finger nectar or pollen in August, and nectar or pollen from a variety of sources from November to January (Figure 3E). Foraging for tawa seed also increased over the November-January period (Figure 3D).

With the exception of Bird 5, birds spent a relatively small proportion of their observed foraging activity taking fruit (Figure 3F). Most birds took hinau and tawa fruit later in the year, but usually they spent <12% of their observed foraging activity on these foods (Figure 3F). Only one bird (Bird 9) was observed taking five-finger fruit (Figure 3F), but nestling faeces frequently contained five-finger seed (*pers. obs.*) indicating that this was fed to nestlings.

Plant phenology and timing of breeding cycle

On Kapiti, most egg laying was recorded in November, irrespective of the intensity of breeding in a given year (Figure 4). As the incubation and nestling periods are 23 (M. J. Sibley *pers. comm.*) and 66 (Moorhouse and Greene, 1995) days, respectively, most breeding birds were feeding nestlings between December and February. The fledgling period extends for a further four months, most fledglings not becoming independent of adults until June (Moorhouse and Greene, 1995).

Of the 19 plant food types for which phenological data are available, 15 were available for at least part of the typical nestling-fledgling period between 1989 and 1992 (Figure 5A-C). However, only hinau seed, tawa seed, wharangi
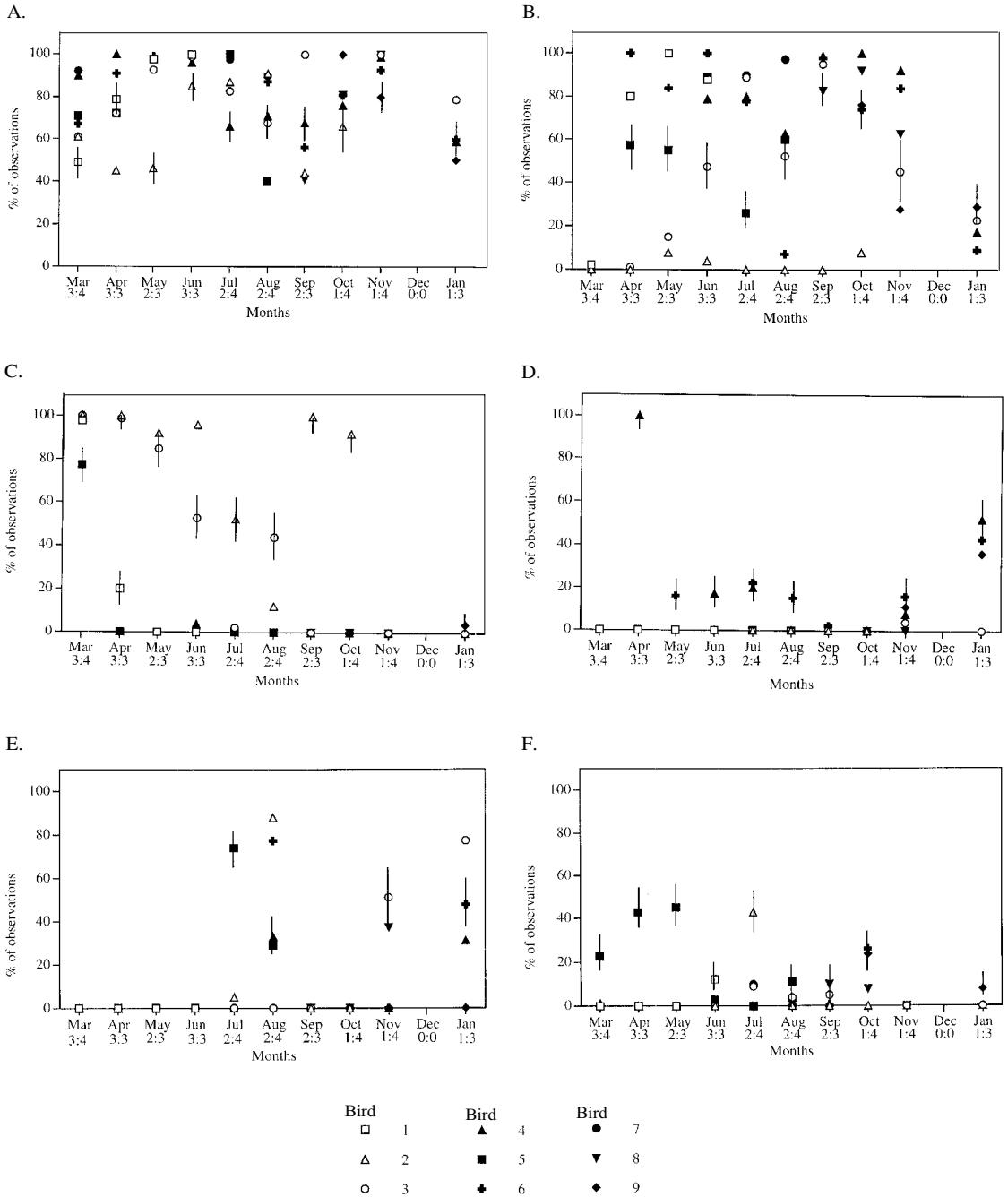
Figure 3: *Seasonal variation in foraging activity of radio-tagged kaka on Kapiti Island between March 1991 and January 1992. Values shown are (A) proportion of total observed activity spent foraging by each bird, and proportion of foraging activity spent feeding on (B) wood or bark dwelling invertebrates, (C) hinau seed, (D) other seeds, (E) nectar or pollen and (F) fruits. White symbols represent males; black symbols represent females. Numbers under months indicate number of males: females observed each month. Vertical bars are the maximum 95% confidence on proportions each month.*

Table 3: *Variation in breeding intensity of North Island kaka on Kapiti Island in five successive breeding seasons.*

	Breeding season				
	1988	1989	1990	1991	1992
No. nests found	23	8	10	3	7
No. known nest sites monitored	0	23	23	23	8
Active nest sites, %	–	35	44	13	88
Nests in which nestlings starved, %	0	38	40	no data	0

seed, five-finger fruit and pigeonwood fruit were present over most of the typical nestling-fledgling period (Figure 5A-C).

Hinau seed was an important food for the majority of the radio-tagged birds observed in March 1991, including the one bird that was feeding a fledgling at this time (Figure 3C). Tawa seed was also taken by the majority of radio-tagged birds observed in January of 1992 (Figure 3D). Five-finger fruit was only taken by one radio-tagged bird, but it was frequently identified in nestling faeces.

The temporal variation in the availability of pukatea seed is unknown, since it was taken by Bird 4 when she was feeding young (Figure 3D), this could potentially be an important food for breeding birds. Pukatea was also a common species on Kapiti (*pers. obs.*). An additional common species which could provide an important food source for breeding birds is kiekie (*Freycinetia banksii*). Kiekie did not flower in 1991 but kaka were observed eating both the flowers and the fruit during the 1994 breeding season (I. Castro *pers. comm.*).

Comparison of breeding intensity on Kapiti Island in five successive breeding seasons indicated
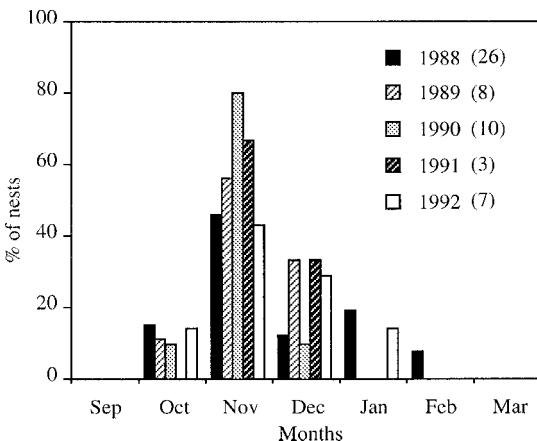
that the years in which most breeding attempts occurred were relatively infrequent (Table 3). The fact that starved nestlings were not observed in the 1988 (Moorhouse, 1991) or 1992 (S. Gibbs *pers. comm.*) breeding seasons (Table 3) suggests that food was more abundant in those years. Unfortunately, the availability of plant food was not quantified during the nestling periods of these breeding seasons.

Discussion

Much of the variation in the foraging activity of individual birds was probably due to the fact that they were not all observed at the same time of year and consequently had access to a different range of plant food. Another potential source of bias could arise through variation in the spread of the sampling effort. Repeated sampling bouts would be expected to produce a more variable picture of foraging behaviour than a single bout simply because the former occur over a longer time interval. The apparent lack of such bias in the results was probably due to the low variation in the number of sampling bouts, or that sampling efficiency (and hence the number of sampling bouts required) was primarily affected not by the diversity of food taken but by the patchiness of specific food types in the environment.

All but one radio-tagged bird spent a minimum of 40% of observed foraging activity feeding on WBI, indicating that this was the predominant foraging activity of kaka on Kapiti over most of the year. Searching for and extracting WBI was also the most frequently observed foraging activity of South Island kaka in broad-leaved rainforest (O'Donnell and Dilks, 1994) and in beech forest (Beggs and Wilson, 1991). Although sap-feeding was only infrequently observed, its apparent restriction to females is consistent with observations of South Island kaka (Wilson *et al., in press*).

The proportion of time birds spend foraging as opposed to other activities provides an indication of how easily they can meet their energy and nutritional
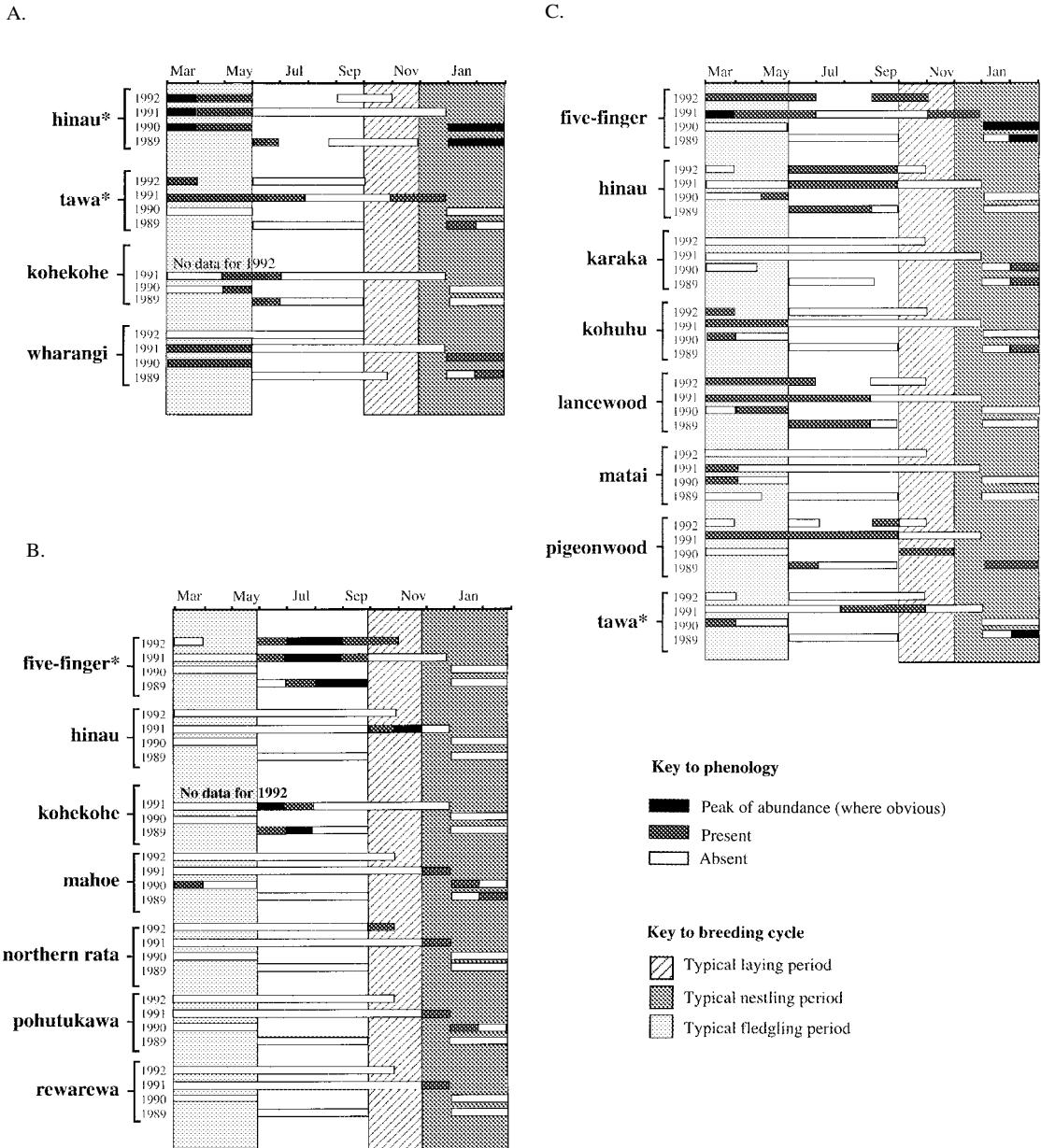

Figure 4: *Timing of the peak of laying in North Island kaka on Kapiti Island in five successive breeding seasons. Numbers in parentheses indicate the number of known nest sites found active each year.*

Figure 5: *Phenology of (A) seeds, (B) nectar or pollen sources and (C) fruits of native plant species eaten by kaka on Kapiti Island in four successive years. Horizontal bars represent the phenology in each year. Gaps indicate periods for which no data were collected or when the phenology could not be reliably extrapolated between surveys. Items marked * were eaten by most radio-tagged birds in the period March 1991 to January 1992.*

requirements. Monthly changes in the proportion of foraging activity observed are difficult to interpret because they could indicate changes in both food quality (or abundance) and nutritional requirements. The general increase in the proportion of foraging relative to other activities from March to June could reflect the increased nutritional demands of the moult between May and August (Moorhouse and Greene, 1995), or decreasing food abundance/quality. A change in either food abundance, quality, or nutrient requirements is supported by the fact that the bird which spent the least time foraging during this period was one which took supplementary food. The general increase in the proportion of foraging activity from September to November could have occurred because birds were attempting to gain condition for breeding. The low incidence of social activity suggests that non-breeding kaka are essentially solitary, at least during daylight hours when the radio-tagged birds were observed.

Since the months in which birds fed predominantly on WBI were generally those in which they spent a relatively large proportion of time foraging, it is likely that feeding on invertebrates is time-consuming compared to foraging on nectar or seeds. Beggs and Wilson (1987) calculated that kaka expend more energy extracting the wood-boring larvae of the coleopteran *Ochrocydus huttonii* than they gain from eating them. This suggests that kaka forage for WBI only when alternative sources of fat and protein, such as seeds, are unavailable (Beggs and Wilson, 1987). On Kapiti the most successful forager for WBI spent only 2% of observed foraging activity (189 observations) eating the invertebrates it found, the remaining time was spent searching for and extracting them from wood or bark. The relative inefficiency of foraging for WBI is supported by the fact that the decline in the proportion of time birds spent foraging from November to January coincided with a dietary shift from WBI to tawa seed and nectar.

Although most radio-tagged birds foraged predominantly for WBI over most of the year, hinau seed was the single most important food source of all birds located in a single month and, for at least some males, in several months. It is possible that the abrupt decrease in the frequency of foraging for hinau seed observed in females in April was due to a more preferred food becoming available. However, the endocarp of hinau fruit hardened considerably between March and April (*pers. obs*.). In March I could extract seed from hinau fruit with my fingers but by April I generally required a hammer to do so. Female kaka have a significantly shorter, shallower

upper mandible than males (Moorhouse *et al., in press*; Wilson *et al., in press*), and it is possible that they were unable to extract hinau seed after the endocarp has hardened. Similar apparent sexual differences in foraging ability have been observed in South Island kaka, where only males appear capable of extracting the wood-boring coleopteran larvae which provide the majority of the fat and protein in the birds' diet (Beggs and Wilson, 1991).

Many seeds, like invertebrates, are relatively high in fats, but are probably considerably less energetically expensive for kaka to obtain. In March 1991 kaka processed (extracted and ingested) an average of 7.1 hinau seeds per minute (95% confidence limits = 4.9 - 9.8, n = 6), the slowest forager spending 87% of observed foraging activity (77 observations) actually processing seed as opposed to searching for it. The only bird that was feeding young foraged exclusively for hinau and pukatea seed until her fledgling was independent, which suggests that it is more efficient to provide young with these foods than WBI.

As none of the radio-tagged birds nested during the study, and only one was feeding a fledgling from the previous breeding season, my available information on the diet of breeding birds is inadequate to identify which plant food types are important determinants of breeding success on Kapiti. It is possible that entirely unknown food types comprise the major part of the diet of breeding birds, particularly those feeding nestlings on which I have no dietary information apart from the fact that five-finger seed was present in nestling faeces. Nonetheless, it is worthwhile to evaluate the potential of known food types as food sources for nestlings and fledglings. Food types most likely to be provided to nestlings and fledglings are those which:

a) are available during all or most of the nestling period,
b) are relatively common,
c) were important in the diet of radio-tagged birds.

Of the known common food plants of kaka on Kapiti for which phenological data are available, hinau, tawa, five-finger, pigeonwood and wharangi produced fruits or seeds over most of the nestling-fledgling period. While wharangi was relatively local in distribution (*pers. obs*.), hinau, tawa, five-finger and pigeonwood are common species on Kapiti (Esler, 1967) and could therefore provide widely distributed and abundant food sources for nestlings and fledglings. Hinau and tawa seeds were important seasonal foods of the radio-tagged birds, while five-finger fruit is known to be fed to

nestlings. Although I have no data on plant food abundance in the peak 1988 and 1992 breeding seasons, the fact that starvation of nestlings was only observed in the intervening seasons suggests that food was more abundant in these years.

The diet of North Island kaka on Kapiti Island was similar to that of South Island kaka in the broadleaf rainforests of South Westland; which is mainly comprised of WBI, seeds, nectar or pollen, fruits and sap (O'Donnell and Dilks, 1994). Although the diet of kaka on Kapiti was more diverse than that in beech forest (Beggs and Wilson 1991), there are some general similarities. On Kapiti, as in South Island beech forest (Beggs and Wilson, 1991), kaka foraged predominantly for WBI, even though this seems energetically expensive for the birds. Seeds, which appear to be essential for breeding in beech forest habitats, also appeared to be important food of kaka on Kapiti. Since both hinau (Daniel, 1978) and tawa (Leathwick, 1984; West, 1986) periodically produce unusually abundant seed crops, reliance on these as the primary food sources of young could explain the annual variation in breeding intensity on Kapiti.

The overlap between the diets of kaka on Kapiti and possums suggests that there is potential for significant food competition between these species in broadleaf-mixed hardwood forests. In addition to reducing the abundance of some kaka food plant species (Kean and Pracy, 1953; Mason, 1958; Meads, 1976; Coleman et al., 1980), possums can severely suppress seed production in both hinau (Cowan and Waddington, 1991) and tawa (Fitzgerald, 1976; Cowan, 1990; Brockie, 1992). Both of these appear to be important food plants of kaka on Kapiti. The restriction of kaka to podocarp and beech forests on the main islands of New Zealand (C. F. J. O'Donnell pers. comm.) could be because these are the only remaining forest types which produce periodically superabundant seed crops (Beveridge, 1964; Wardle, 1984) that are not limited by possums or other introduced herbivores.

Although clutch size, or the number of broods produced, often varies with food abundance in birds, it is unusual for an altricial species to not even attempt to breed in most years (Martin, 1987). The apparent dependence of kaka on infrequently available food crops for nesting could be due to competition from widespread introduced competitors such as rats. However, in a comprehensive analysis of the life-history characteristics of 123 North American passerines and woodpeckers, Martin (1995) found that low fecundity, particularly in terms of the number of broods produced per season, was typical of species with high adult survival and prolonged parental care.

Kaka (Moorhouse and Greene, 1995) and kakapo (Powlesland et al., 1992) both have nestling and fledgling periods lasting several months. Annual adult survival of kakapo has been conservatively estimated at 98% (Clout and Craig, 1995). A female kaka reached the age of 27 years on Kapiti (P. W. Daniel pers. comm.) and the seven adults and twelve juveniles banded between 1988 and 1991 which regularly visit the supplementary feeding station were all still alive in 1995 (P. W. Daniel pers. comm.). This suggests that survival of both adult and young kaka is high. This combination of life-history characteristics suggest that the reduced fecundity of these species could be an integral part of their biology.

Given the apparent dependency of kaka and kakapo on periodically superabundant food crops for successful breeding, trees which periodically produce superabundant seed crops may have played a major role in the evolution of their reproductive biology. Although there is sufficient evidence for a relationship between breeding intensity and full-mast seeding events in kaka, kakapo and yellow-crowned parakeets, the cues that actually induce these species to nest remain obscure. Since all three species begin nesting before the food in question is available (Powlesland et al., 1992; Elliott et al., 1995; Wilson et al., in press), eating these foods cannot directly induce nesting.

Although kaka eat very few plant foods apart from fruit, seeds and nectar, it has been suggested (Wilson et al., in press) that they may be able to detect hormonal indicators of seed production in sap. This hypothesis could explain the apparent restriction of sap-feeding to female birds which, because they make a greater investment in reproduction, would be expected to have a greater interest in predicting the abundance of the food sources that are critical for the survival of young. Captive kaka are capable of nesting every year on a completely artificial diet (M. J. Sibley pers. comm.), which suggests that adequate nutrition alone is sufficient to induce nesting. Nesting could therefore be triggered by an increase in the nutrient content of sap, rather than plant hormones, in full-mast seeding years. As full-mast seeding events are closely correlated with specific climatic conditions (Silvertown, 1980), a general increase in the nutrient content of different types of plant food may occur in a full-mast seeding year. This could explain the initiation of nesting in kakapo which feeds predominantly on leaves and other vegetative plant parts prior to nesting.

The fact that supplementary feeding does not appear sufficient to induce nesting in wild kaka (Wilson et al., in press) or kakapo (G. P. Elliott pers. comm.) argues against improved nutrition as the cue

for nesting. However, it is possible that either the quantity or quality of supplementary food provided in each case was insufficient to induce breeding. Further research is required to identify the factor(s) which induce nesting in these species. Low fecundity is not necessarily disadvantageous in kaka given their life-history characteristics. Since predation of nesting females by stoats is the primary threat to the survival of kaka populations, infrequent nesting has probably reduced the exposure of females to these predators. Concentrating predator control in years when most breeding attempts occur is probably the most cost-effective management strategy for kaka.

Acknowledgements

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