

Intraspecific variation in the foraging ecology of kea, the world's only mountain- and rainforest-dwelling parrot

Amanda L. Greer^{1*}, Gyula K. Gajdon² and Ximena J. Nelson¹

¹School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, 8140, New Zealand

²Messerli Research Institute, University of Veterinary Medicine Vienna, Veterinärplatz 1, 1210 Vienna, Austria

*Author for correspondence (Email: manda.greer@gmail.com)

Published online: 23 April 2015

Abstract: Intraspecific variation can have important knock-on effects on population dynamics and ecosystem processes. There are good indicators that intraspecific differences may exist in the foraging ecology of kea parrots (*Nestor notabilis*). Kea breed in two markedly different habitats (alpine and temperate rainforest), and have pronounced sexual size dimorphism of their upper bill, which may indicate niche partitioning between the sexes. Additionally, as a long-lived species, they can potentially acquire a vast amount of information regarding food sources within their environment, suggesting variation between age classes. We used field observations and faecal analysis to investigate the foraging ecology of kea. We found evidence of invertebrate foraging significantly more frequently in temperate rainforest than in alpine regions, where kea foraged more frequently on fruit. In the alpine habitat, kea fed mainly on fruit during summer and autumn, changing primarily to leaves during winter and spring and increasing invertebrate consumption in springtime. Although there was no discernible impact of sex, we found that adult males foraged more on roots and invertebrates than immature kea, possibly because they were able to exploit a more varied diet through experience. Future research should investigate the relationship between invertebrate foraging and breeding ecology in kea.

Keywords: behavioural ecology; bird; diet; *Nestor notabilis*; niche partitioning; ontogeny; Psittaciformes

Introduction

Foraging ecology is often described at species level. This implies that individuals are ecologically equivalent, possibly obscuring intraspecific variability (see Bolnick et al. 2003). There are many potential causes for intraspecific variation in foraging ecology. For example, living in different habitats may necessitate different diets (Belmaker et al. 2012), different age or sex classes may have different physiological needs (Navarro et al. 2010), and dominant individuals may be able to access more highly valued foods than their subordinates (Prop & Deerenberg 1991). Additionally, dietary choices may vary seasonally. Intraspecific variation can have large-scale impacts on population dynamics and ecosystem processes; consequently to properly understand the role played by a species within its ecosystem(s) it is important to know how that species' foraging ecology varies at different ecological levels (see Hughes et al. 2008). Here we present detailed foraging data on the kea (*Nestor notabilis*), an endangered (Robertson et al. 2013) parrot (Psittaciformes) endemic to the South Island of New Zealand for which circumstantial evidence suggests intraspecific variation at a variety of ecological levels.

Often referred to as the 'world's only alpine parrot' (Diamond & Bond 1999; Young et al. 2012), the majority of kea live in the alpine and subalpine zones of New Zealand's Southern Alps (700–2000 m above sea level (a.s.l.); Robertson et al. 2007) where their habitat comprises alpine grasslands, subalpine scrublands, southern beech forests (*Fuscospora* spp. and *Lophozonia menziesii*), bare rock and scree. The alpine climate is more extreme than in the rest of the country, having stronger winds, lower temperatures and semi-permanent snow reaching down to c. 1000 m during winter (NIWA 2014a). However, some kea breed almost at sea level in New

Zealand's temperate rainforest. These broadleaved-hardwood forests are dominated by rimu (*Dacrydium cupressinum*), kāmahī (*Weinmannia racemosa*), Southern rātā (*Metrosideros umbellata*), and silver beech (*Lophozonia menziesii*). Snowfalls here are rare, and mean maximum daily temperatures vary by just 8°C across the year (NIWA 2014b). Breeding kea usually remain within 1.5 km of their nest (Wilson 1990) meaning that, at least for a portion of the year, many adults likely forage exclusively within the rainforest. Fledglings, however, disperse more widely, with individuals tracked to both habitats (J. Amey, New Zealand Department of Conservation, pers. comm.) and recent work suggests that this population is not genetically isolated (Dussex 2014).

Kea have a highly generalist, omnivorous diet (Brejaart 1988). They explore their environment with innate curiosity and intelligence to exploit all potential food stuffs (Diamond & Bond 1999; Auersperg et al. 2011). Although they seem mainly herbivorous (estimates range from 70% (Brejaart 1988) to 95% (Clarke 1970)), foraging predominantly on fruits and leaves (Jackson 1960; Young et al. 2012), they are one of only two species of parrot (the other being the Antipodes Island Parakeet, *Cyanoramphus unicolor*; Greene 1999) that have been reported to hunt and kill other vertebrates (e.g. Hutton's shearwater (*Puffinus huttoni*) chicks and mice; Pullar 1996; Beggs & Mankelov 2002). The only study to investigate the kea's diet in the rainforest identified nectar/flowers, invertebrates and seeds as their main foods (O'Donnell & Dilks 1994). Notably, although the study was year-round, there were no instances of frugivory and few leaf-feeding observations (4%), suggesting a substantial difference in the foods taken by kea in the rainforest as compared with alpine zones. Fruit in this rainforest is scarce during spring and summer, whereas leaves and invertebrates could provide a more reliable year-

round source of food (O'Donnell & Dilks 1994).

Complex learned behaviours improve with experience and thus with age (Rosenzweig & Bennett 1996). The considerable breadth of the kea's diet and the often harsh nature of the alpine environment require kea to retain a great deal of information about potential food sources within their habitat. Typically, older birds are more successful or efficient foragers than their immature counterparts, but the effects of dominance and/or increasing bill size can be difficult to disentangle from those of age (Desrochers 1992; Riotte-Lambert & Weimerskirch 2013). Kea are an ideal species in which to study age effects because older birds are not necessarily more dominant (Tebich et al. 1996; Diamond & Bond 1999). Also, as the kea's bill attains more than 96% of its adult size by the time individuals fledge (ALG unpubl. data), age differences in bill size are unlikely to have a significant impact on their food handling capabilities. When Diamond and Bond (1991) investigated the foraging behaviour of kea at an open-air rubbish dump (now closed) they found that fledglings were the most inefficient foragers (time eating /time searching) and adults were the most capable of finding new foods. In a natural environment, the skills involved in digging up roots and extracting invertebrates from wood and under rocks may match those displayed in uncovering food from garbage, enabling adults to exploit their environment more effectively than immature kea.

The male kea's bill is much longer (13%) than the female's, yet males are only c. 5% larger in other linear measures of body size (Bond et al. 1991). Sexual size dimorphism (SSD) is often attributed to sexual selection; however, ecological causes, such as niche partitioning, have also been proposed, particularly when the trophic organ is dimorphic (Shine 1989), and have been convincingly demonstrated for some species (e.g. purple-throated carib hummingbirds (*Eulampis jugularis*), Temeles et al. 2000; and house finches (*Carpodacus mexicanus*), Badyaev et al. 2000). It has been suggested that the bill SSD of kea and their only extant congener, the kākā (*Nestor meridionalis*), has an ecological cause, as both species are monogamous and non-territorial (Bond et al. 1991; Moorhouse et al. 1999; but see Székely et al. 2004). Moorhouse et al. (1999) point specifically to the prolonged male provisioning of females and young in these species, and propose that their bill SSD enhances the males' provisioning power. Only male kākā excavate kānuka longhorn larvae (*Ochrocydus huttoni*) or crack hīnau (*Elaeocarpus dentatus*) seeds once these have hardened (Beggs & Wilson 1991; Moorhouse 1997). To date there is no evidence to support ecological causes for bill SSD in kea, at least in part because sexual differences in the diet or foraging behaviour of kea have not yet been investigated.

Here we examine the kea's diet and foraging behaviour in detail using a dataset from alpine and rainforest habitat along the Southern Alps. We predict that: (1) kea in the rainforest will forage less on fruit than those in alpine regions; (2) fruit foraging will decrease in winter and spring, at which time there will be a parallel increase in the amount of foraging on leaves; (3) adults will spend more time eating hard-to-find foods such as roots and invertebrates than immature kea; (4) male kea will be more efficient foragers than females and/or will access resources that females cannot.

Methods

Study sites

Alpine study sites were located at Mount Arthur (41°13' S, 172°40' E; 1700 m a.s.l.), Death's Corner (42°54' S, 171°34' E; 950 m a.s.l.), Hawdon Valley (42°57' S, 171°46' E; 1150 m a.s.l.), Craigieburn (43° 6' S, 171°42' E; 1300 m a.s.l.) and Red Tarns (43°44' S, 170° 5' E; 1050 m a.s.l.). Okarito and surrounds (43°13' S, 170°10' E; 50 m a.s.l.) represented the rainforest habitat. Study sites were chosen to span most of the kea's habitual elevational range. Figure 1 shows the location and types of data recorded at each study site. The season in which these data were collected and the age and sex of each kea sampled are detailed in online Table S1 (Supplementary Material).

Foraging observations

Between October 2010 and July 2012 we filmed (Sony Handycam HDR-XR200VE) 85 kea foraging sessions >1 min long (total c. 600 min) at alpine locations (Fig. 1). Foraging sessions began when a focal kea engaged in a foraging action and ended when no foraging action had occurred for >1 min. Foraging actions consisted of (1) feeding actions: eating fruit, leaves/leaf-buds, flowers, roots, stems, invertebrates/meat, other, unidentified and (2) searching actions: scouting (terrestrial locomotion between two foraging actions, e.g. walking, hopping), digging, overturning rocks, ripping bark and nibbling. We preferentially recorded individuals already foraging. As we were interested in quantifying the kea's natural diet, we only recorded foraging on anthropogenic foods if a

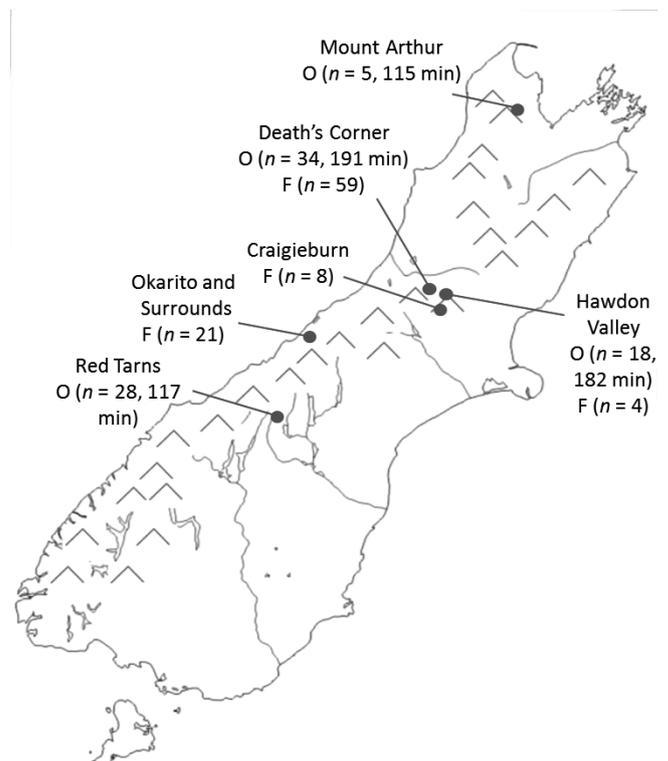


Figure 1. Map of New Zealand's South island, showing study site locations and numbers and types of data on kea (*Nestor notabilis*) collected from each: O – foraging observations, F – faecal samples. Minutes indicate total time of observations.

bird moved from eating natural to anthropogenic food within the same foraging session. Foraging observations <1 min long and opportunistic observations of kea foraging outside of our study sites were included in the list of all foods kea were observed eating or which occurred in their faeces (Table S2), but were not analysed further.

Many observed kea were banded and individually identifiable. Where birds were not banded, age (by degree of yellow colouration on head and bill): nestling, fledgling, juvenile, subadult, adult; and sex (by sexual dimorphism of bill length) could often be distinguished (see Diamond & Bond 1999). We combined subadult observations ($n = 2$) with those of juveniles due to few observations and similar behaviour.

Video footage was analysed using JWatcher 1.0 (Blumstein et al. 2010). Additional foraging sessions begun by the same bird within 15 min of another were pooled. If a group was being recorded, up to but not exceeding half of the birds were excluded from analysis. Individually identifiable birds or those distinguishable by age and/or sex were preferentially retained for analysis; otherwise excluded birds were chosen randomly. Statistical analyses were based on the proportion of time (in seconds) engaged in the behaviour while in sight of the observer.

We analysed observation data using one-way analyses of variance (ANOVAs) to investigate seasonal differences in foraging behaviour and 3×2 factorial ANOVAs to examine the impact of age (fledgling, juvenile, adult) and sex. We split our data analysis in this fashion, rather than using a season \times age \times sex design, because of low sample sizes in the autumn ($n = 6$) and winter ($n = 5$) seasons. Instead, we confined our age and sex analyses to summer ($n = 56$) and excluded the category 'adult female' due to low sample size ($n = 1$). All statistical analyses were conducted using a quasi-binomial distribution because our data were proportional and over-dispersed. The 11 behavioural categories on which ANOVAs were carried out were established a priori (Table 1) and do not include all potential foraging actions. We used Benjamini and Hochberg's (1995) procedure ($\alpha = 0.05$) to control the false discovery

rate (FDR) associated with multiple testing. We report FDR adjusted p -values as q -values throughout. All ANOVAs and q -values were calculated directly in R version 2.15.3 (R Core Team 2013), and over-dispersion was determined using the R package 'AER' (Kleiber & Zeileis 2008).

Faecal analysis

Faecal samples were collected when kea were handled for banding, when they were observed defecating, or when the samples were obviously very fresh (kea droppings are easily identifiable, see Young et al. 2012). Faecal analysis, while having its own limitations (see Putman 1984), can add to the list of known kea foods taken in different seasons and give an indication of the frequency with which a food is eaten so long as that food is reliably passed in an identifiable form (e.g. fruit seeds, cuticular remains of invertebrates). We collected 93 faecal samples, 55 from individually identifiable birds, 16 from unbanded birds of known age and/or sex, and 22 from unknown kea. Most ($n = 71$) samples were collected in the alpine habitat, with 22 samples collected in the rainforest. As nestlings are directly provisioned by adults, these two age categories were combined into a single adult/nestling category. In one instance, faecal samples were collected from both an adult female and her nestling so we excluded the nestling sample in order to avoid pseudo-replication, leaving 21 rainforest samples. Each sample was poured into a Petri dish overlaid on a 0.5-cm² grid and teased apart under a dissecting microscope. Contents were identified, where possible, to species level, using a combination of plant samples collected in the field and seed reference collections (Webb & Simpson 2001; Young 2012); or were grouped into broader categories, such as 'invertebrates' and 'woody material'. Woody material is likely ingested when kea rip apart wood in the search for invertebrates. We used Pearson's chi-square tests to investigate the effects of season, habitat (alpine, rainforest), age (fledgling, juvenile, adult/nestling) and sex on the occurrence of fruit seeds, fruit skin/pulp, invertebrate remains, and woody material within faecal

Table 1. Seasonal variation in the percentage of time in sight of the observer that was spent engaged in foraging actions. Efficiency = total feeding time / total searching time. *Reported as number of species and items eaten per minute. False discovery rate adjusted p -values are reported as q -values, d.f. = 3, 81.

	Seasonal variation		Spring ($n = 18$)		Summer ($n = 56$)		Autumn ($n = 6$)		Winter ($n = 5$)	
	F	q	\bar{x} %	SD	\bar{x} %	SD	\bar{x} %	SD	\bar{x} %	SD
Feeding actions										
Fruit	9.73	<0.001	0	0	38.4	36.9	27.7	40.3	0	0
Flower	1.37	0.536	0.8	2.9	2.8	11.4	0	0	0	0
Leaves/Leaf-Buds	20.82	<0.001	30.4	34.7	2.8	9.6	0.8	2.0	39.7	24.1
Roots	0.31	0.878	7.8	17.5	1.0	5.0	2.8	4.4	0	0
Stems	0.40	0.878	2.0	5.8	0.7	3.3	0.8	1.9	0	0
Searching actions										
Digging	3.44	0.099	7.6	12.5	7.3	18.0	26.6	21.8	2.9	6.5
Overturning	0.52	0.853	3.0	12.2	4.9	15.2	3.0	7.2	0.4	0.9
Rocks										
Scouting	3.95	0.072	16.3	8.9	9.1	9.8	19.2	15.6	27.8	28.3
Efficiency	1.19	0.613	5.3	10.8	34.5	73.6	18.7	44.7	16.8	29.4
Number of species*	1.72	0.403	0.4	0.5	0.4	0.4	0.7	0.7	0.6	0.4
Number of items*	1.54	0.466	1.7	1.0	1.3	3.3	0.5	0.5	0.7	0.1

samples. FDR q -values were used to determine statistical significance. All chi-square tests were conducted using SPSS Statistics 21 (IBM Corporation, NY 10589, USA).

Results

Foraging activity budget

Of their total foraging time, kea spent 65% feeding, and 35% searching for food. Kea ate fruit (47% of feeding time, $n = 39$), leaves/leaf-buds (27%, $n = 28$), invertebrates/meat (10%, $n = 3$), flowers (5%, $n = 14$), roots (5%, $n = 11$), stems (2%, $n = 8$), other foods (1%, $n = 6$) and, in 20 instances (3%), food that could not be identified. Scouting comprised 45% of searching time ($n = 72$), with digging 31% ($n = 33$), overturning rocks 17% ($n = 21$), ripping bark 5% ($n = 1$), and nibbling 2% ($n = 21$) comprising the remainder.

Habitat differences

Kea in alpine zones fed on over 30 species of plant, in addition to unidentified grasses and herbs, invertebrates, the tail of a brushtail possum (*Trichosurus vulpecula*), and anthropogenic foods (listed in Table S2). Figure 2 illustrates the feeding time spent eating each food with >1% of feeding time. A quarter of feeding time was spent eating just *Podocarpus nivalis* fruit or leaves/leaf-buds. Kea were not confined to eating native plants, spending almost a quarter of their feeding time eating various introduced species. We divided the alpine daisy *Celmisia spectabilis* into two categories – ‘in flower’ (3%) and ‘in seed’ (3%) – because up to 97% of *Celmisia* spp. seedheads can host adult and larval seed predators (Molloy 1975), which may provide kea with an additional source of protein.

We recorded at least 27 plant species, invertebrates, moss and woody material in faecal samples collected in alpine regions (Table S2). The most commonly occurring species were: *Coprosma intertexta* (51%), *Coriaria sarmentosa* (11%), *Coprosma cheesmanii* (11%), *Podocarpus nivalis* (11%), *Astelia* spp. (10%), *Phyllocladus alpinus* (7%), *Gaultheria depressa* (7%), and *Coprosma pseudocuneata* (6%). All other species were found in fewer than 5% of the samples.

At least 12 plant species, invertebrates, moss, lichen and woody material were found in faeces collected in the rainforest (Table S2). Seven of these plants (*Aciphylla*

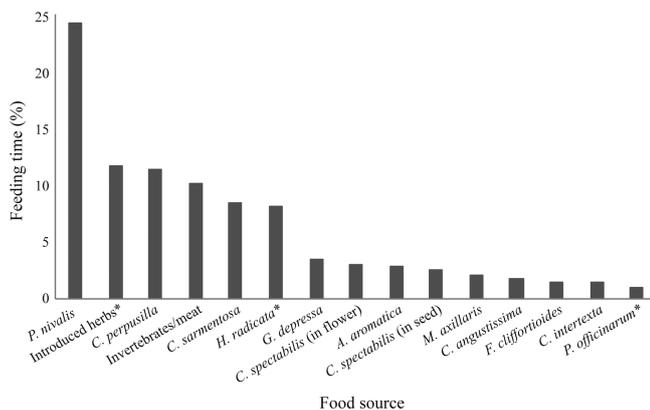


Figure 2. Foods on which kea (*Nestor notabilis*) in alpine regions of New Zealand’s South Island spent >1% of their feeding time. *Introduced species.

spp., *Coprosma intertexta*, *Dracophyllum* spp., *Gaultheria depressa*, *Lepidothamnus laxifolius*, *Phyllocladus alpinus*, *Podocarpus nivalis*) were not known to be eaten by kea in the rainforest habitat. The most commonly occurring plants were *Dracophyllum* spp. (16%), *Gaultheria depressa* (8%), and *Aciphylla* spp. (8%). All others were found in fewer than 5% of samples.

Faeces collected at alpine sites contained fruit seeds (73%; $\chi^2 = 6.70$, $q = 0.048$) more often than did those collected in the rainforest (43%; Fig. 3). Conversely, rainforest samples contained invertebrate remains (71% v. 25%; $\chi^2 = 14.96$, $q < 0.001$) more frequently and woody material (38% v. 15%; $\chi^2 = 5.05$, $q = 0.057$) marginally more frequently than alpine samples. There was no difference between the two habitats in the occurrence of fruit skin/pulp (alpine: 75%; rainforest: 52%; $\chi^2 = 3.80$, $q = 0.102$).

Seasonal differences

The time kea spent eating fruits and leaves/leaf-buds varied seasonally (Fig. 4). More time was spent eating fruit in summer and autumn and more time eating leaves/leaf-buds in winter and spring. There were no other significant seasonal differences in kea diet or behaviour, although the time spent scouting approached significance, with kea tending to move about least during the summer and most during the winter (Table 1). Faecal samples collected in spring contained invertebrates almost three times more frequently than those collected in other seasons ($\chi^2_3 = 24.49$, $q < 0.001$; Fig. 5). Fruit seeds ($\chi^2_3 = 9.40$, $q = 0.057$) and fruit skin/pulp ($\chi^2_3 = 10.33$, $q = 0.051$) tended to occur most frequently in samples collected in the autumn and least frequently in those collected during spring. The occurrence of woody material ($\chi^2_3 = 4.93$, $q = 0.236$) did not vary seasonally.

Age and sex differences

Adult males spent more time eating roots than did juveniles or fledglings, but there were no other age or sex differences in feeding actions (Table 2). When searching, fledglings spent less time scouting for food than juveniles or adult males (Table 2).

Invertebrate remains occurred more frequently in faecal samples from adults/nestlings than from any other age class ($\chi^2_2 = 8.78$, $q = 0.048$; Table 3). There were no further age or sex differences in faecal sample contents (Table 3).

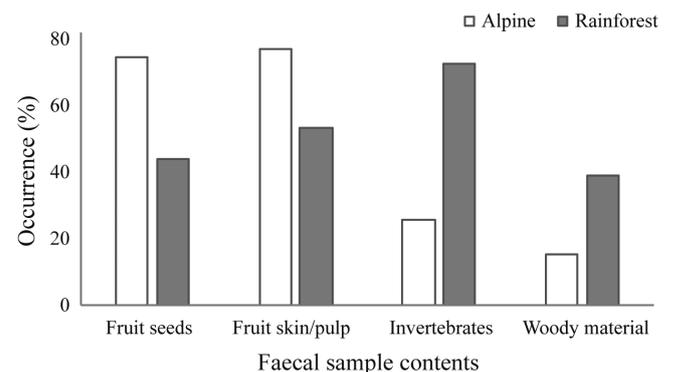


Figure 3. Frequency of occurrence of components related to fruit or invertebrate foraging in kea (*Nestor notabilis*) faecal samples from alpine and rainforest sites on New Zealand’s South Island.

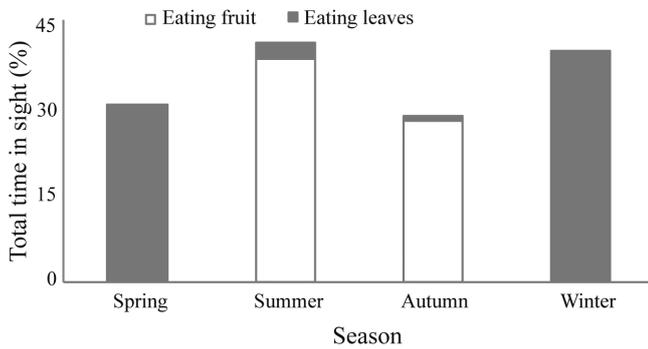


Figure 4. Seasonal variation in the time kea (*Nestor notabilis*) in alpine regions of New Zealand’s South Island spent eating fruit and leaves/leaf-buds.

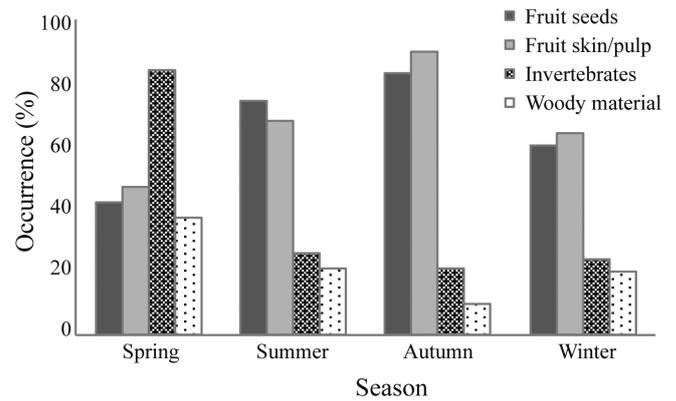


Figure 5. Seasonal occurrence of components related to fruit or invertebrate foraging in kea (*Nestor notabilis*) faecal samples collected from alpine and rainforest sites on New Zealand’s South Island.

Table 2. Age and sex differences in the percentage of time in sight of the observer that was spent engaged in foraging actions. Efficiency = total feeding time / total searching time. *Reported as number of species and items eaten per minute. False discovery rate adjusted *p*-values are reported as *q*-values, d.f. for age = 2, 32; sex = 1, 31. All interactions were non-significant (*q* > 0.05).

Behaviour	Age		Sex		Fledgling (n = 27)		Juvenile (n = 16)		Adult (n = 12)		Male (n = 28)		Female (n = 7)	
	<i>F</i>	<i>q</i>	<i>F</i>	<i>q</i>	\bar{x} %	<i>SD</i>	\bar{x} %	<i>SD</i>	\bar{x} %	<i>SD</i>	\bar{x} %	<i>SD</i>	\bar{x} %	<i>SD</i>
Feeding actions														
Fruit	0.87	0.674	0.68	0.674	45.9	38.9	45.9	33.8	13.0	27.4	28.8	35.1	45.9	39.5
Flowers	3.86	0.132	2.48	0.320	0.9	4.6	0.1	0.5	10.5	22.3	4.5	15.2	3.7	8.9
Leaves/leaf-buds	3.34	0.180	0.06	0.878	1.8	5.0	0.5	1.4	7.7	18.7	4.7	13.0	2.5	4.3
Roots	6.45	0.041	0.01	0.935	0.1	0.8	0.1	0.6	4.0	10.4	1.8	6.9	0.6	1.5
Stems	2.62	0.267	7.01	0.072	0.2	0.8	1.7	5.7	0.6	2.2	0.4	1.6	3.9	8.5
Searching actions														
Digging	0.19	0.878	2.73	0.300	6.1	17.7	7.7	19.3	9.1	17.8	6.1	13.2	2.0	2.3
Overturning rocks	0.40	0.853	0.11	0.878	7.6	20.0	0.6	2.2	0.5	1.6	0.3	1.1	1.4	3.2
Scouting	10.59	< 0.001	3.65	0.218	6.0	8.2	11.8	12.0	12.4	8.7	10.1	8.2	14.5	15.8
Efficiency	1.13	0.618	0.27	0.853	44.7	73.5	41.1	94.2	5.4	7.0	29.0	74.3	40.7	67.7
Number of species*	0.06	0.937	0.25	0.853	0.6	0.6	0.4	0.3	0.3	0.2	0.3	0.2	0.5	0.4
Number of items*	0.76	0.717	0.71	0.674	3.1	6.6	0.8	1.0	0.8	0.6	0.9	0.8	1.4	3.6

Discussion

We found that kea in alpine regions spent most time eating fruit, followed by leaves/leaf-buds, and animal matter. Reinforcing this finding, faeces collected in alpine areas contained evidence of fruit foraging almost three times as often as invertebrate foraging (leaf and other plant organ remains were too digested to be reliably quantified). In contrast, faecal samples collected in the rainforest contained invertebrate remains more frequently than fruit remains. This suggests a large difference between the diets of kea in these habitats. Although O’Donnell and Dilks’ (1994) rainforest study confirmed kea feeding on invertebrates for only 13% of their observations, they also recorded a further 32% of ‘probable invertebrate’ observations. Thus invertebrate foraging likely accounted for almost half of their observations, versus just 4% of fruit and leaf feeding observations combined. A substantially increased amount of animal protein in the kea’s diet could have significant impacts on their breeding ecology. Nestlings of frugivores that are also

fed invertebrates may both grow and fledge more quickly (Roca 1994). Another New Zealand parrot, the yellow-crowned parakeet (*Cyanoramphus novaezelandiae*), which forages heavily on invertebrates is thought to breed much earlier and have a longer lasting breeding season than the closely related, but predominantly herbivorous, red-crowned parakeet (*C. auriceps*; Greene 1998).

In alpine areas, kea spent almost a quarter of their feeding time eating the fruits and leaves of *Podocarpus nivalis*, making this species by far the most handled food source. Various *Coprosma* species were also among the most handled species and commonly occurred in faecal samples, thus our results agree with previous literature, which has noted *P. nivalis* and a variety of *Coprosma* species as being the mainstay of kea frugivory (Jackson 1960; Clarke 1970; Young et al. 2012). In addition, though *P. nivalis* is a true alpine plant and is not known to grow in the Westland rainforest (New Zealand Plant Conservation Network, accessed 5 June 2014), its remains were also found in a faecal sample collected in the rainforest,

Table 3. Percentage of kea faecal samples containing material related to fruit or invertebrate foraging by age (d.f. = 2) and sex (d.f. = 1). False discovery rate adjusted *p*-values are reported as *q*-values.

	Age		Sex		Fledgling (<i>n</i> = 19)	Juvenile (<i>n</i> = 21)	Adult/ nestling (<i>n</i> = 30)	Male (<i>n</i> = 39)	Female (<i>n</i> = 19)
	χ^2	<i>q</i>	χ^2	<i>q</i>	%	%	%	%	%
Fruit seeds	1.61	0.511	1.99	0.231	68	57	50	67	47
Fruit skin/pulp	5.17	0.133	0.01	0.944	84	57	53	64	63
Invertebrates	8.78	0.048	1.12	0.357	26	24	60	46	32
Woody material	0.28	0.928	2.04	0.231	26	24	20	15	32

indicating that at least one (subadult, female) kea fed in both alpine and rainforest habitats during winter.

Large seasonal differences were noted in the kea's diet, such that fruit-feeding was most common during the summer and autumn. However, the presence of fruit seeds in winter and spring faecal samples revealed that kea were still eating some fruit throughout the year, taking advantage of both late-remaining berries, and late-fruiting species, such as *Coprosma intertexta*. Leaf/leaf-bud feeding increased substantially during the leaner months of winter and spring and invertebrates were eaten far more frequently during spring than any other season. Seasonal variations in diet have been found in other parrots, with increased invertebrate foraging noted as coincident with the breeding season (e.g. Smith & Moore 1991), or pre/post breeding season (e.g. Díaz & Peris 2011). For kea, increased invertebrate foraging coincides with the post-hatching, pre-fledging phase of chick development. This differs from kākā and the other member of the Strigopoidea family, the kākāpō (*Strigops habroptila*), which raise chicks during summer and only breed in years when trees are mast-fruiting or -seeding (Powlesland et al. 2009). This suggests that kea may maintain their annual spring chick-rearing cycle by increasing the level of animal protein in their diet.

Adult kea spent more time eating roots than immature birds, and their faeces contained more invertebrates and woody material. These differences can be attributed to increased experience, as adult and immature kea have similar bill sizes and adults do not have preferential access to highly-prized foods (Tebbich et al. 1996; Diamond & Bond 1999). Roots and many invertebrates require extracting, meaning an extra step before the 'hidden' food can be obtained (King 1986). This additional complexity may take practice to master. Adult brown capuchin monkeys (*Cebus apella*) are more efficient extractive foragers than juveniles as they search more effectively (Gunst et al. 2010), whereas, failing to restrict searches to specific areas, juvenile wandering albatross (*Diomedea exulans*) are the least successful foraging class (Riotte-Lambert & Weimerskirch 2013). We found no difference in the time kea spent digging by age class, yet we only observed one instance of a fledgling actually eating roots and this bird was eating what remained in a hole already dug by another kea. Our results suggest that either the searching or excavating abilities of younger birds do not yet equal those of adults.

If ecological factors are the driving or maintaining force behind the kea's bill sexual size dimorphism (SSD), we would have expected males to differ from females in one of the following ways: be more efficient foragers; take more food items; exploit more species; or exploit a resource inaccessible to females, or for a longer period of time, or to a greater

extent than females. We found no differences in the foraging ecology of male and female kea; however, we must offer two caveats to these results. Firstly, we were constrained by our observational data to analysing sex and age differences in the summer months only. Intraspecific differences in alpine regions may be at a minimum at this time of year due to an abundance of readily available berries. Any enhanced male provisioning ability may only be apparent during the colder months, when the male's longer bill could make it a more powerful or efficient digging/prying tool in hard, frozen ground, or in deep snow. This coincides with the period when females are incubating eggs or raising chicks and increased male foraging ability would be particularly advantageous. Secondly, we had insufficient summertime foraging observations of adult females to include in our analysis, which may have impacted on our ability to detect age and sex differences in the diet of kea, particularly as adult females form a unique category with the specific physiological requirement of egg-laying. However, our faecal sample analysis, which did not suffer from these limitations, revealed no differences in invertebrate or fruit foraging between males and females. Székely et al. (2004) and Serrano-Meneses and Székely (2006) found that sexual selection rather than niche partitioning was the most likely explanation for SSD within largely monogamous and non-territorial seabird taxa. Here we found no evidence for an alternative explanation for kea.

In conclusion, there is a great degree of intraspecific variation in the foraging ecology of kea, which seems mainly driven by season and habitat type, with age playing a more minor role. Future research should investigate the potential impact of a diet substantially richer in animal protein on kea breeding ecology, particularly breeding season timing and length, and nestling growth rates.

Acknowledgements

We are grateful to the Department of Conservation Franz Josef Kea Team, and to Ria Brejaart, Raoul Schwing, Sasha Roselli, Laura Young, Ian Warrington, Alan Woods, Andrius Pašukonis and the members of the Arthur's Pass KCT Survey Teams 2011/2012 for their valuable assistance, and two anonymous referees for their constructive comments. We thank the Department of Conservation (National Permit Numbers WC-30391-FAU & WC-30527-FLO) and the University of Canterbury Animal Ethics Committee (Approval No. 2010/19R) for permission to conduct this research. We acknowledge the use of species occurrence data drawn from the National Vegetation Survey Databank (NVS). This research

was funded by the Miss E.L. Hellaby Indigenous Grasslands Research Trust, the Brian Mason Scientific & Technical Trust Fund, and the Royal Forest and Bird Protection Society of New Zealand. ALG was supported by a University of Canterbury, School of Biological Sciences Doctoral Scholarship.

References

- Auersperg AMI, von Bayern AMP, Gajdon GK, Huber L, Kacelnik A 2011. Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi access box paradigm. *PLoS ONE* 6(6): e20231.
- Badyaev AV, Hill GE, Stoehr AM, Nolan PM, McGraw KJ 2000. The evolution of sexual size dimorphism in the house finch. II. Population divergence in relation to local selection. *Evolution* 54: 2134–2144.
- Beggs W, Mankelov S 2002. Kea (*Nestor notabilis*) make meals of mice (*Mus musculus*). *Notornis* 49: 50.
- Beggs JR, Wilson PR 1991. The kaka *Nestor meridionalis*, a New Zealand parrot endangered by introduced wasps and mammals. *Biological Conservation* 56: 23–38.
- Belmaker J, Sekercioglu CH, Jetz W 2012. Global patterns of specialization and coexistence in bird assemblages. *Journal of Biogeography* 39: 193–203.
- Benjamini Y, Hochberg Y 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)* 57: 289–300.
- Blumstein DT, Daniel JC, Evans CS 2010. JWatcher™. <http://www.jwatcher.ucla.edu/>.
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulseley CD, Forister ML 2003. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* 161: 1–28.
- Bond AB, Wilson K-J, Diamond J 1991. Sexual dimorphism in the kea *Nestor notabilis*. *Emu* 91: 12–19.
- Breijaart R 1988. Diet and feeding behaviour of the Kea (*Nestor notabilis*). Unpublished dissertation, Diploma in Parks and Recreation Management, Lincoln University, Canterbury, New Zealand.
- Clarke CMH 1970. Observations on population, movements and food of the kea (*Nestor notabilis*). *Notornis* 17: 105–114.
- Desrochers A 1992. Age and foraging success in European blackbirds: variation between and with individuals. *Animal Behaviour* 43: 885–894.
- Diamond J, Bond AB 1991. Social behavior and the ontogeny of foraging in the kea (*Nestor notabilis*). *Ethology* 88: 128–144.
- Diamond J, Bond AB 1999. Kea, bird of paradox: the evolution and behavior of a New Zealand parrot. Berkeley, CA, University of California Press. 230 p.
- Díaz S, Peris S 2011. Consumption of larvae by the Austral Parakeet (*Enicognathus ferrugineus*). *The Wilson Journal of Ornithology* 123: 168–171.
- Dusseix N, Wegmann D, Robertson BC 2014. Postglacial expansion and not human influence best explains the population structure in the endangered kea (*Nestor notabilis*). *Molecular Ecology* 23: 2193–2209.
- Greene TC 1998. Foraging ecology of the red-crowned parakeet (*Cyanoramphus novaeseelandiae novaeseelandiae*) and yellow-crowned parakeet (*C. auriceps auriceps*) on Little Barrier Island, Hauraki Gulf, New Zealand. *New Zealand Journal of Ecology* 22: 161–171.
- Greene TC 1999. Aspects of the ecology of Antipodes Island Parakeet (*Cyanoramphus unicolor*) and Reischek's Parakeet (*C. novaeseelandiae hochstetteri*) on Antipodes Island, October–November 1995. *Notornis* 46: 301–310.
- Gunst N, Boinski S, Fragaszy DM 2010. Development of skilled detection and extraction of embedded prey by wild brown capuchin monkeys (*Cebus apella apella*). *Journal of Comparative Psychology* 124: 194–204.
- Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M 2008. Ecological consequences of genetic diversity. *Ecology Letters* 11: 609–623.
- Jackson JR 1960. Keas at Arthur's Pass. *Notornis* 9: 39–58.
- King BJ 1986. Extractive foraging and the evolution of primate intelligence. *Human Evolution* 1: 361–372.
- Kleiber C, Zeileis A 2008. *Applied econometrics with R*. New York, Springer. ISBN 978-0-387-77316-2. <http://CRAN.R-project.org/package=AER>.
- Molloy BPJ 1975. Insects and seed production in *Celmisia*. *Canterbury Botanical Society Journal* 8: 1–6.
- Moorhouse RJ 1997. The diet of the North Island kaka (*Nestor meridionalis septentrionalis*) on Kapiti Island. *New Zealand Journal of Ecology* 21: 141–152.
- Moorhouse RJ, Sibley MJ, Lloyd BD, Greene TC 1999. Sexual dimorphism in the North Island Kaka *Nestor meridionalis septentrionalis*: Selection for enhanced male provisioning ability? *Ibis* 141: 644–651.
- Navarro J, Oro D, Bertolero A, Genovart M, Delgado A, Forero MG 2010. Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird. *Marine Biology* 157: 2453–2459.
- NIWA 2014a. Mountainous/Alpine regions: Mount Cook. www.niwa.co.nz/education-and-training/schools/resources/climate/overview/map_alpine (accessed 8 April 2014).
- NIWA 2014b. Database: Mean daily maximum temperatures (°C) 1981–2010, <http://www.niwa.co.nz/education-and-training/schools/resources/climate/maxairtemp> (accessed 8 April 2014).
- O'Donnell CFJ, Dilks PJ 1994. Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. *New Zealand Journal of Ecology* 18: 87–107.
- Powlesland RG, Greene TC, Dilks PJ, Moorhouse RJ, Moran LR, Taylor G, Jones A, Wills DE, August CK, August ACL 2009. Breeding biology of the New Zealand kaka (*Nestor meridionalis*) (Psittacidae, Nestorinae). *Notornis* 56: 11–33.
- Prop J, Deerenberg C 1991. Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19–28.
- Pullar T 1996. Kea (*Nestor notabilis*) captive management plan and husbandry manual. Threatened Species Occasional Publication 9. Wellington, Department of Conservation. 15 p.
- Putman RJ 1984. Facts from faeces. *Mammal Review* 14: 79–97.
- R Core Team 2013. R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing. <http://www.R-project.org>.
- Riotte-Lambert L, Weimerskirch H 2013. Do naive juvenile seabirds forage differently from adults? *Proceedings of the Royal Society B: Biological Sciences* 280: 20131434. doi:10.1098/rspb.2013.1434

- Robertson CJR, Hyvonen P, Fraser MJ, Pickard CR 2007. Atlas of bird distribution in New Zealand, 1999–2004. Wellington, Ornithological Society of New Zealand Inc. 533 p.
- Robertson HA, Dowding JE, Elliott GP, Hitchmough RA, Miskelly CM, O'Donnell CFJ, Powlesland RG, Sagar PM, Scofield RP, Taylor GA 2013. Conservation status of New Zealand birds, 2012. New Zealand Threat Classification Series 4. Wellington, Department of Conservation. 22 p. + supplementary data.
- Roca RL 1994. Oilbirds of Venezuela: ecology and conservation. Cambridge, MA, Nuttall Ornithological Club Publication 24.
- Rosenzweig MR, Bennett EL 1996. Psychobiology of plasticity: Effects of training and experience on brain and behavior. *Behavioural Brain Research* 78: 57–65.
- Serrano-Meneses M-A, Székely T 2006. Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. *Oikos* 113: 385–394.
- Shine R 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *The Quarterly Review of Biology* 64: 419–461.
- Smith GT, Moore LA 1991. Foods of corellas *Cacatua pastinator* in Western Australia. *Emu* 91: 87–92.
- Székely T, Freckleton RP, Reynolds JD 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proceedings of the National Academy of Sciences (USA)* 101: 12224–12227.
- Tebbich S, Taborsky M, Winkler H 1996. Social manipulation causes cooperation in keas. *Animal Behaviour* 52: 1–10.
- Temeles EJ, Pan IL, Brennan JL, Horwitt JN 2000. Evidence for ecological causation of sexual dimorphism in a hummingbird. *Science* 289: 441–443.
- Webb CJ, Simpson MJA 2001. Seeds of New Zealand gymnosperms and dicotyledons. Christchurch, Manuka Press in cooperation with the Caxton Press. 428 p.
- Wilson K-J 1990. Kea, creature of curiosity. *Forest & Bird magazine* 21: 20–26.
- Young LM 2012. Seed dispersal mutualisms and plant regeneration in New Zealand alpine ecosystems. PhD thesis, University of Canterbury, Christchurch, New Zealand. <http://hdl.handle.net/10092/6992>.
- Young LM, Kelly D, Nelson XJ 2012. Alpine flora may depend on declining frugivorous parrot for seed dispersal. *Biological Conservation* 147: 133–142.

Editorial Board member: Jo Monks

Received 16 July 2014; accepted 1 March 2015

Supplementary Material

Additional supporting information may be found in the online version of this article:

Table S1. Numbers of field observations and faecal samples of kea (*Nestor notabilis*) collected in each habitat (alpine/rainforest; South Island, New Zealand) by season, sex and age.

Table S2. List of foods kea (*Nestor notabilis*) in both habitats (alpine/rainforest) were observed eating or which occurred in faecal samples.

The *New Zealand Journal of Ecology* provides online supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.