Alpine flora may depend on declining frugivorous parrot for seed dispersal

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ABSTRACT

Globally, bird numbers are declining, with potentially serious flow-on effects on ecosystem processes, such as seed dispersal mutualisms. However, management to maintain seed dispersal may be inappropriate if unexpected animals are the most important dispersers. Numbers of the world's only alpine parrot, the New Zealand kea (*Nestor notabilis*), have declined drastically over the last 120 years after an intense period of official persecution. Today <5000 kea remain in the wild. Previously it has been assumed that like other parrots, kea would destroy most of the seeds they eat, thereby contributing little to seed dispersal. The New Zealand alpine flora is rich in fleshy-fruited species yet has a limited disperser fauna. Consequently, we investigated the relevance of kea as a seed disperser in New Zealand's alpine ecosystems. Field-based foraging observations coupled with faecal analyses showed kea were by far the most important extant alpine avian frugivore. Kea selected more fruiting species (21 vs. 17 species), consumed more fruit, and dispersed more seeds (8137 vs. 795) than all other birds combined. Rates of seed predation by kea were extremely low, and evident in only 25% of species eaten. Kea are the only species that make frequent long-distance flights within and between mountain ranges. Hence, much of the effective long-distance dispersal of the alpine flora may be currently performed by kea. Conservation of kea is therefore important both for ensuring the survival of the species and for their role in seed-dispersal mutualisms for which there are few extant substitutes.

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1. Introduction

Understanding the role of mutualists within natural communities is important for predicting how their decline might alter plant communities (Anderson et al., 2011; Christian, 2001), and for associated conservation and management purposes (Garcia et al., 2010; Trakhtenbrot et al., 2005). In addition to the global decline in the number of bird species, the number of individuals is estimated to have declined 20–25% in the last five centuries (Gaston et al., 2003). Avian populations and dependent ecosystem services are therefore probably declining faster than predicted by species extinctions because of "functional extinction" (Sekercioglu et al., 2004). Seed dispersal is one of the most influential avian ecological services (Howe and Smallwood, 1982; Sekercioglu et al., 2004). Globally, dispersal failure may be an increasing problem for many plant species (Christian, 2001; Corlett, 1998; Traveset and Riera, 2005), yet the botanical implications of avian frugivore extinctions and declines are poorly understood (Cordeiro and Howe, 2001).

Few studies experimentally link bird declines with plant declines (but see Anderson et al., 2011; Wenny et al., 2011; Wotton and Kelly, 2011 for evidence supporting this). New Zealand offers

an excellent opportunity to understand the ecological consequences of bird declines, with only the "wreckage of an avifauna" (Diamond, 1984) remaining in an island situation that, barring three bat species, evolved without terrestrial mammals. Plant-animal mutualisms in New Zealand have almost certainly undergone major changes since the arrival of humans and the subsequent extinction or decline of many bird and lizard species (Holdaway, 1989; Towns and Daugherty, 1994; Kelly et al., 2010). Almost half (41%) of the endemic avifauna has gone extinct (Innes et al., 2010), including a number of known frugivores (Holdaway et al., 2001). Weakened pollination mutualisms in forest communities have already been demonstrated as an example of flow-on effects of bird decline in New Zealand (Anderson et al., 2011), and there is also concern about dispersal failure affecting large-fruited trees (Wotton and Kelly, 2011). Before human arrival in 1280 AD (Wilmshurst et al., 2008), birds were the major seed dispersers (Lord, 2004), with minor local contributions by lizards (Whittaker, 1987; Wotton, 2002) and invertebrates such as weta (Orthoptera) (Duthie et al., 2006).

Alpine ecosystems can be considered as naturally fragmented landscapes; spatially segregated 'islands' separated by seas of lower elevational forest (Halloy and Mark, 2003), analogous to indigenous forest remnants in a matrix of agricultural land. Dispersal of seeds between alpine areas is thus important for facilitating genetic connectivity between fragmented patches,

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maintaining metapopulation persistence, and promoting long-term species survival. In New Zealand's alpine areas, which constitute around 13% of the total land area, little is known about animal–plant dispersal mutualisms. Fleshy-fruitedness is unusually common (12%) in the New Zealand indigenous alpine flora compared to other temperate alpine plant communities (e.g. fleshy fruited species represent 3–5% of the alpine flora in Victoria, Australia and 5.4% in Chile) (Lord, 1999 and references therein). However, despite the preponderance of fleshy-fruited alpine species, there are few extant frugivores to disperse the seeds.

The kea (*Nestor notabilis*) is the world's only alpine parrot and is potentially the only remaining significantly frugivorous bird that lives and feeds in New Zealand's alpine zone (Bull, 1965; Clarke, 1970). (Note: for Maori names like kea, the plural does not take an "s"). Kea eat the fruit of a range of alpine plant species (Clarke, 1970; Jackson, 1960; Breejart, 1988). These large, long-lived birds can fly long distances (c. 20–30 km) within and between different mountain ranges (Clarke, 1970; Elliott and Kemp, 2004). Worldwide, parrots are primarily seed predators (see Boyes and Perrin, 2010 and references therein) and, while seed predation has typically been assumed for kea (Clout and Hay, 1989; Willson et al., 1989; Lee et al., 1991; O'Donnell and Dilks, 1994), evidence on seed survival after kea ingestion is scarce.

Kea populations have undergone very large declines because of an intensive campaign of official persecution, prompted by occasional kea attacks on farm animals (Marriner, 1908). This is one of the worst cases of avicide in New Zealand's recent history. From the late 1800s, the government placed a bounty on kea beaks. In the 1920s, the bounty was 10 shillings per beak, equating to $65 (NZD) today (Temple, 1996). This provided a clear incentive to kill birds even in protected areas (Pullar, 1996). Only in 1971, after an estimated 150,000 kea had been killed (Cunningham, 1948) did the bounty cease. In 1986 kea were finally given full protection, but some individuals are still destroyed if they are known to attack sheep. Currently, only an estimated 1000–5000 individuals remain in the wild (Anderson, 1986). Kea are listed as an 'at risk' species by the New Zealand Department of Conservation (DoC) (Miskelly et al., 2008) and 'vulnerable' by the IUCN (2010) and numbers continue to decline (DoC and Kea Conservation Trust, unpubl. data). In addition to illegal hunting and pet trade activities, other major threats to kea populations include predation, competition for resources with introduced mammals and humans, lead poisoning from anthropogenic causes, and habitat degradation (Pullar, 1996).

We tested to what extent kea ingest and defecate intact seeds from various plant species, and their relative importance for seed dispersal in the alpine zone. We quantified: (i) the relative numerical contribution to frugivory and seed dispersal by kea compared with other birds in the alpine zone, (ii) what plant species kea fed on, and how this compared to fruit availability, and (iii) whether kea provided a high quantity and quality of dispersal through the proportion of seeds ingested and dispersed intact.

2. Methods

2.1. Study species and sites

Kea measure 45–50 cm in length (mean weight: 780 and 960 g for females and males, respectively) and live in complex, stratified social systems (Diamond and Bond, 1999). They typically live between 700 m and 2000 m in altitude in the Southern Alps of New Zealand, a habitat composed predominantly of southern beech (*Nothofagus*) forest and alpine grasslands (Jackson, 1960). Kea feed on a range of food items, including invertebrates and fruit, leaves, roots and flowers of over 100 plant species (Breejart, 1988). Kea tend to form larger flocks from January (Jackson, 1960; Clarke,

1970) and forage above the treeline during the summer period before dispersing into smaller flocks in autumn and retreating to lower altitudes during winter (Jackson, 1960).

Our two study sites were about 180 km apart in the Southern Alps: Red Tarns, Mt Sebastopol, Mt Cook National Park (43°45′S, 170°6′E, 1000–1300 m a.s.l.) and Mt Sugarloaf, Cass, <5 km east of the Arthurs Pass National Park eastern boundary (43°2′S, 171°4′E, 1000–1360 m a.s.l.). These sites were chosen because prior research established that these were important feeding areas for kea, which came from, and returned to multiple mountain ranges surrounding these mountains. There are no data on kea densities in these areas; however, both areas are known to be strongholds for kea. Feeding observations took place above the treeline in the subalpine zone consisting of scrub, shrubland, and grassland, with bare rock and scree habitat at both sites. At least 50 fleshy-fruited species within 24 genera and 14 families occurred at the sites (see Appendix, Table A1 for fruit trait details for most of these species). The fruit of some species ripens as early as December, with the peak fruiting season from January until May, although many fruits remain on plants over winter. We use the term "fruit" here in a functional sense to encompass seeds enclosed in or associated with a fleshy edible structure (e.g. drupes, berries or arils), i.e. species with seeds that are dispersed by passage through an animal's gut. We use the term "alpine" to represent any habitat occurring above treeline (approximately 1100 m a.s.l).

2.2. Feeding observations

2009 fruiting season: To determine which bird species were present and feeding in alpine areas, we made foraging observations of birds other than kea ("non-kea feeding observations") during the 2009 fruiting season. Alpine habitats consist of low, open vegetation, making it easy to detect birds at large distances (often > 300 m) and to observe them with binoculars without apparent effects on their behaviour. We slowly walked a similar route at Sugarloaf over ten non-consecutive days between January and April during the alpine fruiting season, before autumn snowfall. The route varied among days within a larger available foraging area on the mountain, guided by where fruiting species were located. Walks usually took 2–3 h, covering ca. 3–5 km, stopping periodically to scan with binoculars, and were equally divided between the most active foraging periods in mornings (6–11 am) and evenings (4–9 pm) (Jackson, 1960) (although seldom within the same day). Every time we encountered a bird, we noted the food item eaten (plant, insect or other). We recorded the total number of observations for each bird species feeding on each food type (Galetti, 1993).

2010 fruiting season: We used the same methods as above to collect bird (non-kea) feeding observations between January and April 2010. Additionally, because the 2009 observations showed kea were important and very mobile dispersers, we incorporated kea-focused feeding observations when kea were encountered during these sessions (January–May 2010). Morning and evening kea-feeding observations were conducted for 10 days at each site and most sampling days fell non-consecutively. When kea were detected, we approached to within 10 m and observed them using binoculars. Kea feeding behaviour was not affected by our presence at these distances, possibly because of their historical lack of predators and neophilia (Diamond and Bond, 1999). The latter is a particularly useful characteristic of these birds that makes them amenable to study (e.g. Gajdon et al., 2004). Between one and three observers were present during each survey period, and usually spread out across the broad foraging area on the mountain to obtain independent samples. Some feeding data were recorded via direct observation while other data were captured using a high definition video (HDV) camera (Canon HV30, 10× optical zoom)

to obtain more detailed feeding behaviour using zoom-in capabilities upon playback. We recorded 229 discrete feeding events (11 h in total), incorporating individuals from both sexes and all age classes, although the majority of our observations were on juveniles and fledglings (see Appendix, Table A2). This preponderance of younger birds matches the age composition of typical kea flocks seen in the alpine areas, probably because young birds flock together to feed above the treeline while breeding adults most likely forage more locally in their territories (B. Barrett pers. comm).

For each feeding event we recorded: time of day (morning or evening), feeding duration (seconds), and food type (plant, insect or other). For plant material we recorded species, and part(s) eaten (fruit, aril, seed, flower, leaf, root, stem, whole or unknown). Finally, for fleshy-fruited species, we noted seed treatment method (ingested or rejected) where possible. One feeding event was classified as a discrete observation of a single bird feeding on a single food item for a certain length of time. If the bird left the plant to feed on a different item, it was recorded as a new event (Galetti, 1993). We tried to avoid sampling the same bird more than once in a session. To minimise pseudoreplication arising from potential group-influenced feeding behaviours, we avoided sampling mulitple birds from within a closely feeding group (especially multiple birds feeding on the same plant). We sampled only during non-rainy days, because we learned from the 2009 season that birds are much less active in the rain.

2.3. Food choice in relation to availability

We measured fruit abundance throughout the fruiting season to establish whether certain species were eaten by kea in proportion to their relative abundance and whether this changed over the fruiting season. We visually scored fruit abundance along thirteen 50 m line transects (six at Red Tarns, seven at Sugarloaf) within the general area where feeding observations were made. We sampled a circular plot using a string of 2 m radius (plot area = 12.56 m^2) every 10 m from 0 to 50 m. Plot centres were marked so the same area could be sampled at each re-measurement period. Within each plot (six per transect), we recorded the percentage vegetation cover of all fleshy-fruited species. For each fleshy-fruited species within the plots we then assigned a relative fruit abundance per unit area score (ranging from 0 to 10, with higher scores indicating higher levels of fruiting). We calculated cover-adjusted fruit abundance scores by multiplying the fruiting score by percent vegetation cover for each species in each plot. Mean fruiting scores were then calculated across plots for each site. To account for temporal variation in fruiting, we scored fruit abundance early, mid and late season and related this to kea fruit-feeding activity around each of those time periods. To have approximately equal numbers of field work days per time period, the data were divided into "early season" – all observations before March 15 (Red Tarns = 57 kea feeding observations, Sugarloaf = 53 observations), "mid season"– March 15–April 13 (Red Tarns = 78, Sugarloaf = 17 observations), and "late season" – April 14–May 6, 2010 (no kea feeding observations).

To determine whether kea feeding changed significantly through the season, we used Generalised Linear Models (GLMs) with a gaussian error distribution for the four most-often eaten plant species to model the proportion of all feeding observations devoted to that species against the explanatory variables season (early or mid) and site (Red Tarns or Sugarloaf). We used the arcsine square root transformation to normalise the proportion of time spent feeding response variable. Three of the four plant species showed significant differences between early and mid season in the proportion of time kea spent feeding on the fruits (*Podocarpus nivalis* $P = 0.003$, *Pentachondra pumila* $P < 0.001$, *Muehlenbeckia axillaris* $P = 0.03$, *Gaultheria depressa* $P = 0.06$, df$_{(1,202)}$). Site effects

were also significant. We therefore kept data for each time period and site separate in the analysis of food choice in relation to availability. GLM's were done using the statistical package R version 2.13.1 (R Development Core Team, 2011).

2.4. Seed treatment

Preliminary observations indicated that when feeding on *P. nivalis*, kea sometimes use their beaks to separate the fleshy red aril from the seed, ingesting the aril and rejecting the seed directly back into or near the parent plant. Consequently, seed fates of *P. nivalis* were impossible to quantify using feeding observations alone. To determine whether rejected seeds were intact or destroyed during this type of feeding, we randomly collected 200 kea-processed *P. nivalis* seeds from the vicinity of three plants at Red Tarns and counted both the number of intact and damaged seeds.

2.5. Faecal sampling and gut-passage time

To determine the effects of gut passage on seed fate and to identify species eaten, we collected all fresh kea faeces ($n = 65$) and all other bird faeces ($n = 35$) found during this survey period. Faeces were searched for repeatedly across all microhabitat types (e.g. under shrubs, on scree slopes) to collect as many faecal samples as possible from all birds. Faeces were analysed for seed species, recording seed numbers per faecal sample and visible condition of seeds (intact or fragmented), using a microscope (6–40 × magnification). Kea faeces are distinguishable from other birds because of the large size, distinctly darker colouring, and the absence of a white uric acid segment produced by most other birds present at these alpine sites. The characteristics of kea faeces were known from faeces produced by kea being handled for banding. Non-kea faeces could not usually be distinguished between bird species; therefore all non-kea bird faeces were collectively referred to as coming from "other birds".

We tested gut passage times using six captive kea at Willowbank Wildlife Reserve, Christchurch, New Zealand. The birds were fed blueberries (*Vaccinium corymbosum*: Ericaceae) because their colour makes them easy to detect in faeces, and fruit have numerous tiny seeds similar to the confamilial *Gaultheria* spp. commonly eaten by wild kea. We recorded the length of time between when kea ate the berries and when they emerged in the faeces, finishing after 4.5 h, when seeds stopped coming through.

2.6. Statistical analysis

We used Ivlev's electivity index (Ivlev, 1961) to calculate kea feeding selectivity ratios (SR). Ivlev's electivity index (E) is defined as: $E = (r - p)/(r + p)$ where r is the proportion of the food item in the diet and p is the proportion of food available in the environment. This provides an index ranging between -1 and $+1$, where values closer to -1 indicate an under-representation and values closer to 1 indicate an over-representation of the food item in the diet compared with the relative availability in the environment. To minimise effects of seasonal changes in fruit availability, selectivity calculations compared diet to availability within early, middle and late season as defined above. Following Forsyth et al. (2002), we used the following breaks for classification; $E > 0.3$, "preferred"; $-0.3 < E < 0.3$, "not selected"; $E < -0.3$, "avoided".

3. Results

3.1. Feeding observations

Twelve of the 20 observation days provided data on kea feeding (six at each site). On the other days, birds were either not present,
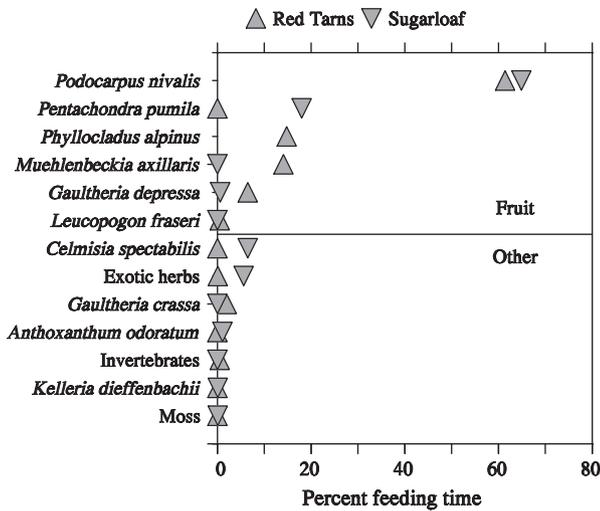
Fig. 1. Percentage of time kea spent feeding on fleshy fruited plant species and other non-fruit food items (leaves, dry seed capsules and/or flowers of other plants). Exotic herbs were *Taraxicum* sp. and *Pilosella* sp., *P. alpinus* was not present at Sugarloaf.

present but not feeding, or feeding but too far away to positively identify foraging behaviour. We recorded a total of 229 discrete feeding observations on all food items (Red Tarns = 141, Sugarloaf = 88), totalling 652.37 min. At Red Tarns most feeding observations were in the mornings (94%), while at Sugarloaf most were in the evenings (82%). Feeding bouts ranged from 2 to 958 s and mean feeding bouts for morning and evening, respectively were: Red Tarns = 208 s and 206 s; Sugarloaf = 44 s and 166 s (see Appendix, Table A2).

We observed kea feeding on 13 different food items, including fruit from six fleshy-fruited plant species (Fig. 1). Numbers of feeding observations were higher on fruit ($n = 205$) than on all other food items ($n = 24$). Moreover, kea spent considerably more time feeding on fruit than on other foods. This was consistent between sites, with 93.7% of the observed feeding time dedicated to frugivory at Red Tarns and 83.5% at Sugarloaf. Five fruiting species were eaten by kea at Red Tarns, compared with only three species at Sugarloaf. All fruiting species eaten were present at both sites except for *Phylloclaudus alpinus*, which was absent at Sugarloaf. Fruits of *P. nivalis* dominated kea diets at both sites, constituting over 60%

of observed feeding time (Fig. 1), and also comprising most of the feeding observations (Red Tarns $n = 91$, Sugarloaf $n = 53$). There were clear differences between sites in the proportion of time spent feeding on other species; e.g. kea fed on *P. pumila* for 18% of the time at Sugarloaf but we never observed this at Red Tarns. Overall, we observed kea eating six of the 19 seed species recorded in kea faeces (see below).

Other bird species were either typically observed feeding on food items other than fruit and/or were rarely seen above the treeline. We observed only eight other native and seven introduced bird species (collectively referred to as "other birds"), which ate relatively little fruit compared with kea (Table 1). Just 12 fruit-feeding events on eight different plant species were seen across all other bird species combined, compared with 205 observations for kea (i.e. kea provided 94.5% of all fruit-feeding observations).

3.2. Food choice in relation to availability

Relative fruit abundance changed throughout the fruiting season and peak fruiting time differed depending on species and site (Table 2). At both sites, all feeding observations took place early and mid season; no kea were seen feeding on fruit late in the season, despite the abundance of ripe fruit in many species. Fruit abundance was not measured during late season at Sugarloaf due to early snowfall. Kea preferred fruits of *P. nivalis*, *P. alpinus*, *M. axillaris* and *P. pumila*. All other fruiting species were eaten less often than expected at both sites, though the faecal samples showed that 19 species in total were occasionally fed on by kea (see below).

3.3. Seed treatment, faecal sampling and gut-passage times

We collected 35 faecal samples in total from other birds. Most (58%) contained insects and 91.4% also contained seeds from a total of 15 different plant species (Table 3). The average number of seeds per sample, irrespective of plant species, was 22.7 (±8.7 se), but most samples (65.7%) contained fewer than 20 seeds each. *Coprosma propinqua* was by far the most commonly eaten fruit, with 74.3% of faecal samples containing at least one *C. propinqua* seed. Seeds of *G. depressa* – the next most abundant species in the faeces – were found in just 14.3% of faecal samples, and were only abundant in one sample (260 seeds ≈ one fruit). Most seeds were intact,

Table 1

Feeding observations for all (non-kea) bird species seen consuming fruit[c] above the treeline in the fruiting seasons of 2009 and 2010, and for kea in 2010, at Arthurs Pass, Cass, and Mt Sebastopol.

Bird species	Number of observations			Published frugivory observations[b]	Fruit spp. eaten (other foods)
	Fruit	Insects	Other		
Kea (*Nestor notabilis*)	205	2	22	Yes[1,2,3]	Table 2
NZ pipit (*Anthus novaeseelandiae*)	3	30	0	No. Mostly insects[4]	*Acrothamnus colensoi, Coprosma perpusilla, Pentachondra pumila*
Silvereye (*Zosterops lateralis*)	2	3	0	Forest plants only[5]	*Coprosma propinqua, Podocarpus nivalis*
Blackbird (*Turdus merula*)[a]	2	2	0	Forest plants only[5]	*Aristotelia fruitcosa, Coprosma propinqua*
NZ falcon (*Falco novaezealandiae*)	1	1	2	Yes[6]	*Leucopogon fraseri*, (lizards, birds)
Tomtit (*Petroica macrocephala*)	1	4	0	Forest plants only[5]	*Coprosma propinqua*
Song thrush (*Turdus philomelos*)[a]	1	3	0	Forest plants only[5]	*Coprosma propinqua*
Canada goose (*Branta canadensis*)[a]	1	0	4		*Coprosma petriei*, (grass)
Chaffinch (*Fringilla coelebs*)[a]	1	2	0	Forest plants only[5]	*Aristotelia fruitcosa*
Rock wren (*Xenicus gilviventrus*)	0	1	0	Yes[7]	None in this study

[a] Exotic species.

[b] Source: 1 = Clarke, 1970; 2 = Campbell 1976; 3 = Breejart, 1988; 4 = Garrick, 1981; 5 = O'Donnell and Dilks, 1994; 6 = Young and Bell, 2010; 7 = Michelsen-Heath and Gaze 2007.

[c] Six bird species were seen eating other food items: Harrier (*Circus approximans*) 7 observations on carrion; Grey Warbler (*Gerygone igata*) 2 on insects; Black-back gull (*Larus dominicanus*) 3 on carrion; Skylark (*Alauda arvensis*)[a] 4 on insects; Magpie (*Gymnorhina tibicen*)[a] 1 on insects and 2 on carrion; Chukar (*Alectoris chukar*)[a] 1 on grass seed.

Table 2

Relative abundance of fruit available in relation to amount eaten by kea throughout the fruiting season and selectivity ratio (SR) using Ivlev's electivity index (*E*). (S) selected—those plant species eaten more than expected from their availability (*E* > 0.3); (N) not selected—those plant species eaten in proportion to their availability; (A) avoided—those plant species eaten less than expected based on their availability (*E* < −0.3). Na means no data; dash means cannot be calculated.

Plant species	Early season			Mid season			Late season		
Red Tarns	% Fruit available	% of time feeding	SR	% Fruit available	% of time feeding	SR	% Fruit available	% of time feeding	SR
Phyllocladus alpinus	0	4	S	0	12	S	0	0	–
Muehlenbeckia axillaris	1	0	A	1	29	S	2	0	A
Podocarpus nivalis	46	92	S	57	49	N	70	0	A
Gaultheria depressa	20	0	A	13	9	N	0	0	–
Leucopogon fraseri	2	0	A	2	1	A	7	0	A
Aristotelia fruticosa	2	0	A	0	0	–	0	0	–
Coprosma parviflora	1	0	A	1	0	A	4	0	A
Pentachondra pumila	29	0	A	27	0	A	16	0	A
Acrothamnus colensoi	0	0	–	0	0	–	0	0	–
Gaultheria crassa	0	4	S	0	0	–	0	0	–
Sugarloaf									
Podocarpus nivalis	48	67	N	51	100	S	Na	0	
Pentachondra pumila	11	32	S	7	0	A	Na	0	
Gaultheria depressa	32	1	A	31	0	A	Na	0	
Acrothamnus colensoi	7	0	A	8	0	A	Na	0	
Leucopogon fraseri	1	0	A	2	0	A	Na	0	
Muehlenbeckia axillaris	1	0	A	1	0	A	Na	0	
Aristotelia fruticosa	0	0	–	0	0	–	Na	0	
Coprosma parviflora	0	0	–	0	0	–	Na	0	
Gaultheria crassa	0	0	–	0	0	–	Na	0	

Table 3

Mean numbers of whole (intact) seeds per faecal sample and percentage intact for seeds found in fecal samples from kea (*n* = 65) and other birds (*n* = 35).

	Kea			Other birds		
	Whole seeds			Whole seeds		
Plant species	Mean (se)	Total seeds	% Intact	Mean (se)	Total seeds	% Intact
Acrothamnus colensoi	6.7 (2.2)	437	100	0.8 (0.6)	34	82.4
Androstoma empetrifolia	0.03	2	100	–	0	–
Aristotelia fruticosa	0.1 (0.1)	9	100	0.1 (0)	5	40
Coprosma cheesemannii	0	0	–	0.8 (0.8)	27	100
Coprosma depressa	1.2 (1.2)	75	100	–	0	–
Coprosma fowerakeri	5 (4.7)	325	100	–	0	–
Coprosma intertexta	2.2 (1.7)	144	100	–	0	–
Coprosma perpusilla	0.5 (0.3)	30	100	–	0	–
Coprosma petriei	2 (1.4)	128	100	0.3 (0.3)	12	100
Coprosma propinqua	2.7 2.7)	177	100	8.2 (2.1)	290	98.6
Coprosma serrulata	0.1 (0.1)	5	100	–	0	–
Coriaria plumosa	0.5 (0.3)	32	96.9	–	0	–
Coriaria sarmentosa	6.1 (2.1)	400	98.8	–	0	–
Corokia cotoneaster	0	0	–	0.3 (0.2)	10	100
Gaultheria depressa	89.5 (36.2)	5817	100	8.3 (7.4)	290	100
Leptocophylla juniperina	0.2 (0.2)	12	100	0.1 (0.1)	3	66.7
Leucopogon fraseri	2.4 (0.7)	158	98.7	0.6 (0.6)	20	100
Muehlenbeckia axillaris	2.3 (0.9)	149	98.7	1.3 (1.3)	46	100
Pimelea sericiovillosa	0.1 (.0.1)	7	71.4	–	0	–
Podocarpus nivalis	3.3 (0.2)	219	99.1	0.2 (0.2)	8	100
Pseudopanax colensoi	0.2 (0.2)	11	100	0.1 (0.1)	5	100
Unidentified sp. A	0	0	–	0	1	0
Unidentified sp. B	0	0	–	0.7 (0.7)	24	95.8
Unidentified sp. C	0	0	–	0.5 (0.5)	18	94.4
Unidentified sp. D	0	0	–	0.1 (0.1)	2	100
		8137			795	

with generally low proportions of seed fragments found overall (Table 3). Overall, small birds were dispersing seeds intact, but in relatively low numbers and from fewer plant species compared with kea.

Seeds and undigested fruit pulp comprised most of the kea faecal content, with few invertebrates or plant foliage present. We recorded three times more fruiting species in kea faeces (*n* = 19, Table 3) than during our feeding observations (*n* = 6, Fig. 1). For

example, various *Coprosma* species and *Acrothamnus colensoi* were very common throughout the faecal samples, even though none were eaten during our observations. Overall, we found extremely low proportions of seed fragments in kea faecal samples, and for most plant species 100% of seeds were excreted intact. Only six of the 19 seed species from kea faecal samples contained some fragments, and all but one species still had at least 96% of the seeds visually intact. Among the 200 rejected *P. nivalis* fruits, we found
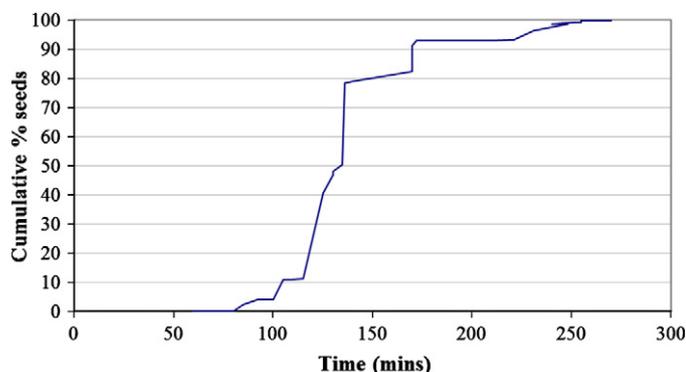
Fig. 2. Cumulative percentage excretion over time (minutes after fruit consumption) of blueberry seeds passing through 33 faeces collected from 6 captive kea at Willowbank Wildlife Reserve, New Zealand.

that 98% were intact and had not been damaged by the beak during feeding.

Captive kea readily ate blueberries and each bird ate 20–30 fruit over a half hour time period. We recovered 33 faeces in total from the 6 birds and counted between 0 and 220 seeds per sample. Gut passage times for blueberry seeds ranged from 85 to 275 min (Fig. 2) with an overall mean seed retention time of 140.4 ± 36.3 min.

4. Discussion

Our data show that not only are kea legitimate seed dispersers, as previously reported by Clarke (1970), but also they are the numerically dominant avian seed disperser for most fruiting species in New Zealand alpine ecosystems. Kea damaged unexpectedly few seeds during feeding and gut-passage. The passage of seeds through the digestive tract is important in determining their future germination behaviour (Traveset et al., 2001) and reproduction ability. Seed dispersal quantity depends on the number of visits a disperser makes and the number of seeds dispersed per visit, while dispersal quality depends on the treatment of seeds in the disperser's mouth and gut and on seed deposition patterns (Schupp, 1993). Our data showed most seeds were defecated intact. Clarke (1970) collected seeds of five species from kea faeces and most of these germinated, but more germination studies on a greater range of alpine plant species are needed to test the effects of kea gut-passage. We have set up germination experiments, but the results are not yet available, as many New Zealand alpine plant species take years to germinate (both for bird-dispersed and hand-collected seeds). To date after 19 months, only C. propinqua has had substantial germination, with kea-dispersed seeds germinating well compared with hand-cleaned seeds and seeds inside whole fruit (30%, 45% and 35% respectively). In general, since scarification effects of gut passage on germination are usually relatively small (Robertson et al., 2006), we would expect intact seeds to germinate well after they have passed through a kea gut.

We observed kea feeding on only one third of the total number of fruiting species found in their faeces. This may reflect the clear preferences by kea for certain fruits, resulting in higher chances of observing kea feeding on these species (e.g. P. nivalis). In other studies kea are reported as feeding on fruits of c. 30 fleshy-fruited species (Clarke, 1970; Jackson, 1960; Breejart, 1988), which – if those seeds are also passed intact – would suggest that kea are likely responsible for the long-distance movement of seed for many more species than we report here.

Work elsewhere shows that animals which eat a small fraction of the seed crop, but have long gut passage times and high mobility, can be very important for long-distance dispersal (Jordano et al., 2007). Kea are the only bird in the New Zealand alpine zone capable of long-distance flights, (Clarke, 1970; Elliott and Kemp, 2004) and have relatively long gut passage times (over 2 h, see results). Kea are thus more likely to disperse seeds longer distances than small passerines, which typically defecate seeds within an hour of ingestion (Murphy et al., 1993; Jordano et al., 2007), often within 20 min (Levey, 1987). Coupled with a long retention time, the frequent long-distance flights made by kea suggest that they are probably the most important long-distance seed disperser of alpine plants. While kea did not disperse all seeds away from the parent plant (e.g. P. nivalis) almost all rejected seeds remained intact, permitting secondary dispersal through other means, such as wind or water.

Given the paucity of bird species in New Zealand's alpine habitat, it is not surprising that we saw so little feeding activity by birds other than kea. Most of the seeds that small birds excreted were from lower-altitude (montane–subalpine) shrub species, some of which also grow beneath the forest canopy (e.g. C. propinqua, Aristotelia fruticosa). Most low-statured, higher-altitude fruiting species were eaten only by kea. Only one other bird species – the endangered rock wren (Xenicus gilviventrus) – lives and breeds exclusively in the alpine zone. While fruits are reported occasionally in rock wren diets (Heather and Robertson, 1996) the distances they move seed is probably limited, as they are poor fliers (Michelsen-Heath and Gaze, 2007). A similar problem besets the New Zealand pipit (Anthus novaeseelandiae), which in our data is the next most important seed disperser after kea, but probably only for localised dispersal events. Other small forest-dwelling passerines (e.g. tomtit, Petroica macrocephala) sometimes feed on fruits above treeline, but feeding visits are likely to be restricted to lower subalpine elevations and therefore probably contribute little to seed dispersal of alpine plants. A rare report of direct frugivory by the New Zealand falcon (Falco novaeseelandiae) – a high-country transient – was given by Young and Bell (2010). While probably uncommon for New Zealand falcons, several overseas examples demonstrate the important contribution by birds of prey to occasional long-distance seed dispersal events through both direct and secondary seed ingestion (Boehning-Gaese et al., 1999; Galetti and Guimarães Jr, 2004; Padilla and Nogales, 2009).

Non-avian fauna may also contribute to alpine seed dispersal, although data are scarce. Lizards provide effective local dispersal of lowland shrubs on offshore islands – in New Zealand (Wotton, 2002) and elsewhere (Olesen and Valido, 2003) – but because of introduced predators lizard density over much of New Zealand is now low, including around Sugarloaf where their role in dispersal of alpine plants was found to be small (Lawrence, 1997). Weta (Orthoptera) can disperse small-seeded native plants over short distances in forests (Duthie et al., 2006) although Wyman et al. (2011) found that most seeds were destroyed in the process. Alpine grasshoppers (L.M.Y. unpubl. data) and scree weta (Larsen and Burns, in press) also disperse tiny seeds of alpine Gaultheria species over short distances. Finally, there are a number of introduced mammals in the New Zealand alpine, including possums (Trichosurus vulpecula), red deer (Cervus elaphus) and chamois (Rupicapra rupicapra) which might eat fruit and disperse some seed, but little is yet known about seed dispersal by larger mammals in New Zealand (Kelly et al., 2010).

Overall, these alpine habitats host a depauperate avian frugivore community despite having many fleshy-fruited plant species, raising evolutionary questions about why this may be so. Some extinct avifauna are likely to have been important for dispersal of alpine plants. Seeds from montane fleshy-fruited

plants have been found in gizzards (Burrows, 1989) and coprolites (Wood et al., 2008) of extinct moa species, and while less is known about the diets of upland moa species, they may also have played a role in long-distance dispersal events if seeds were defecated intact. Horrocks et al. (2008) analysed coprolites of kakapo (*Strigops habroptilus*) – a previously widespread but now critically endangered flightless parrot – and reported seeds from six alpine fleshy-fruited species passed through the gut relatively undamaged. Best (1984) also recorded kakapo feeding on fruits and seeds from alpine plants. Moa and kakapo were historically widespread and could have been important frugivores, making their total and near-extinction (respectively) all the more unfortunate.

The seed-dispersal potential of kea is rather unusual. Parrots are typically significant predators of seed because they feed on the embryo of the fruits they forage on (Collar, 1997), and consequently rarely act as primary seed dispersers (Boyes and Perrin, 2010; Janzen, 1981; Jordano, 1983; Galetti and Rodrigues, 1992). The few seeds that are dispersed after gut-passage are tiny (e.g. neotropical *Ficus* and *Cecropia*) (Janzen, 1981). We know of only two other cases of parrots acting as dispersal agents. Boehning-Gaese et al. (1999) showed that a small proportion of seeds of the Malagasy tree (*Commiphora guillaumini*) handled by the Lesser Vasa Parrot (*Coracopsis nigra*) were carried away from the parent, with resulting higher establishment success as seedlings. Sazima (2008) found in Southeastern Brazil the parakeet *Brotogeris tirica* occasionally carried the seeds of the palm *Syagrus romanzoffiana* up to 40 m away from the parent tree. On a global scale, our study demonstrates that kea have unusual feeding behaviour compared with other parrots.

5. Conservation management and future work

The importance of seed dispersal is being increasingly recognised in conservation management. Seed dispersal helps maintain metapopulation integrity and gene flow between fragmented populations (Hamilton, 1999), such as those on mountain tops. Global warming coupled with anthropogenic habitat modification already poses significant threats to alpine ecosystems (Halloy and Mark, 2003). It is therefore important for long-term plant persistence that dispersal continues to function effectively (Venn and Morgan, 2010). Globally, dispersal failure may be an increasing problem for many plant species (Corlett, 1998; Traveset and Riera, 2005). Although global declines in frugivores may disrupt seed dispersal mutualisms and inhibit plant recruitment, quantifying the likely reduction in plant regeneration is difficult. Seeds that fail to be dispersed may suffer disproportionate mortality beneath parent plants (Janzen–Connell effects) (Janzen, 1970; Connell, 1971). Therefore, dispersal may be required even for local short term persistence. Dwindling kea numbers may negatively affect persistence of fleshy-fruited alpine plant species, especially given the important role of kea in long-distance dispersal events.

Management to maintain seed dispersal mutualisms may be mis-targeted if there is incorrect information about which animals are the most important dispersers. Jordano et al. (2007) showed that in *Prunus mahaleb*, although birds ate most fruits, the largest contribution to long-distance dispersal came from carnivorous mammals. Calvino-Cancela (2002) discovered that gulls, rather than specialist frugivores, were the most effective dispersers in carrying *Corema album* seeds to suitable microsites, while Nogales et al. (1999) demonstrated the quantitative and qualitative effectiveness by common ravens for six plant species in the Canaries.

Loss of these key dispersers, especially in fragmented habitats, could impair seed-mediated gene flow and restrict seed arrival to a subset of local microsites.

Across the Northern Hemisphere, bears can act as seed dispersers, and have experienced widespread, historical persecution events for reasons similar to kea persecution – to prevent them from killing livestock (Zedrosser et al., 2011). The difference is that large carnivore populations are now increasing in many parts of Europe and North America through concerted conservation management efforts, even in areas of high human densities. Kea populations are apparently still declining, despite their legal protection since 1986.

The fact that kea were able to ingest fruit and rarely crushed seeds despite their powerful curved 'parrot' beak is noteworthy. These large birds can damage motor vehicles, buildings and signs, yet they can manipulate delicate items with considerable dexterity. This shows the importance of not pre-judging the role of animals within an ecosystem. The morphology of the beak of the kea (or its relation, the kaka (*Nestor meridionalis*), which is an important and at times delicate pollinator (Kelly et al., 2010)) could lead researchers to dismiss kea as likely seed predators.

To conclude, we have identified kea as an unexpectedly important seed disperser species in an ecosystem that may depend largely on this species for long distance dispersal. This is important, as many areas in the Southern Alps have become degraded over time due to high grazing pressure by introduced ungulates, e.g. deer, chamois, tahr (*Hemitragus jemlahicus*) and goats (*Capra hircus*), and also hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) (King, 2005). Maintaining seed dispersal from more intact sites to recovering high country land (after introduced mammals have been controlled) thus helps ensure ongoing plant regeneration. Germination experiments of kea-dispersed seeds and tests for any Janzen–Connell effects on these species in the alpine zone are needed to further evaluate the risk posed by loss of kea. Habitat restoration should also focus on reversing the kea population decline to ensure both the survival of the species and for its role in maintaining vital ecosystem processes.

Acknowledgements

Appendix A

See Tables A1 and A2.

Table A1

Summary of fruit traits for alpine fleshy-fruited plant species at the study sites. All genera are represented here, but some species with similar fruit traits have been omitted (e.g. *Astelia, Coriaria, Gaultheria, Halocarpus, Lepidothamnus, Rubus, Coprosma, Nertera* and *Pimelea* also include other species that are present above treeline). Measurements include range of length and width (where available) of the diaspore including upper limit dimensions (in brackets).

Family	Species	Colour polymorphic	Fruit colour(s) when ripe	Fruit size (mm)	Diaspore unit	Size of endocarp/pyrene/seed (mm)[a]	Number of seeds[a]
Araliaceae	*Pseudopanax colensoi*	No	Dark purple	8–12	Fleshy exocarp with endocarps	2.9–5	2
Asteliaceae	*Astelia linearis*[b]	No	Red	6–9 × 8–13	Berry	1.4–2.2(–2.4)	1-Numerous
Coriariaceae	*Coriaria plumosa*	No	Purple	6–11 × 6–11	Achenes enclosed in fleshy petals	1.8–2.1	5–10
	Coriaria sarmentosa	No	Purple	6–11 × 6–11	Achenes enclosed in fleshy petals	1.6–2.3	5–10
Elaeocarpaceae	*Aristotelia fruticosa*	Yes	Pink, red, white, black	4–8 × 4–9	Drupe with hard endocarp	2.0–2.6 × 2.0–2.6	1–3
Ericaceae	*Acrothamnus colensoi*	Yes	Red, white, pink	4–6 × 4–6	Drupe with hard endocarp	2.5–3.5 × 2.2–3	3–5 (–6) Filled
	Androstoma empetrifolia	No	Red	3–4 × 3–4	Drupe with hard endocarp	1.6–2.3 × 1.6–2.1	
	Gaultheria antipoda	Yes	White, pink, red	7–13 × 7–13	Capsule with accrescent fleshy calyx	0.5–0.65	>200
	Gaultheria depressa	Yes	White, pink, red	7–13 × 7–12	Capsule with accrescent fleshy calyx	0.4–0.65	>200
	Leptecophylla juniperina	Yes	Red, white	4–7 × 5–9	Drupe with hard endocarp	2–3.5 × 3–5	2–3 (–6) Filled
	Leucopogon fraseri	No	Orange	4–6 × 4–6	Drupe with hard endocarp	2.5–4(5) × 2–2.7	2–4 (–5) Filled
	Pentachondra pumila	No	Dark pink to red	4–7 × 6–10	Drupe with pyrenes	1.6–2.0(–2.2)	5–10
Escalloniaceae	*Corokia cotoneaster*	Yes	Red, orange, yellow	6–10	Drupe with hard endocarp	4.5–6	1
Lobeliaceae	*Pratia angulata*	No	Pinkish purple	8–16	Berry	0.6–0.9	15–40
	Pratia macrodon	No	Purplish	8–16	Berry	0.6–0.8	15–40
Myrsinaceae	*Myrsine nummularia*	No	Bright purple	6–9	Globose drupe	3–4(–4.5) × 2.7–3	1
Phyllocladaceae	*Phyllocladus alpinus*	No	White	7–16	Fleshy aril partly surrounding seed	2.5–2.9(–3.1)	1 seed per aril
Podocarpaceae	*Halocarpus bidwillii*	No	White	3–5 × 1–3	Aril surrounding exposed seed	3–4(–4.5) × 1–2	1 per receptacle
	Lepidothamnus laxifolius	No	Crimson/dark purple	2.5–6	Seed exarillate, with swollen receptacle	4–5	1 per receptacle
	Podocarpus nivalis	No	Red, orange, peach	2.5–10	Seed exarillate with fleshy receptacle	5.5–6.5(–7)	1–2 per receptacle
Polygonaceae	*Muehlenbeckia axillaris*	No	Fleshy white	5–7 × 5–7	Fleshy perianth surrounding nut	2.7–3.9 × 1.5–2.0	1
Roseaceae	*Rubus schmidelioidies*	No	Orange–yellow		Fleshy aggregate of 1-seeded drupelets	1.6–2.7	Many
Rubiaceae[c]	*Coprosma cheesemannii*	No	Bright orange–red	6–7	Pyrenes within a fleshy drupe	3.2–4.2(–4.5) × 2.2–2.7(–3)	(1–)2(–4)
	Coprosma crenulata	No	Bright red	6–8	Pyrenes within a fleshy drupe	3.8–5(–5.5) × 2.5–3.2(–3.5)	(1–)2(–4)
	Coprosma depressa	No	Bright red–orange	5–6	Pyrenes within a fleshy drupe	3.2–4(–4.4) × 1.7–2.2(–2.3)	(1–)2(–4)
	Coprosma dumosa	Yes	White–red–yellow	4.0–7.7	Pyrenes within a fleshy drupe	2.3–3.3 × 2.2–2.8	(1–)2(–4)
	Coprosma fowerakeri	No	Bright orange–red	4–5(6) × 3–5(6)	Pyrenes within a fleshy drupe	3.6–4.6 × 2.2–2.6	(1–)2(–4)
	Coprosma intertexta	Yes	White, pale blue, speckled	4–6	Pyrenes within a fleshy drupe	2.1–4.1 × 1.8–2.4	(1–)2(–4)
	Coprosma niphophila	No	Orange–red	5.8–10 × 5.8–8	Pyrenes within a fleshy drupe	3–3.3 × 2.1–2.2	2
	Coprosma perpusilla	No	Orange–red	4–7.5(11) × 5–6.8	Pyrenes within a fleshy drupe	2.2–2.7 × 1.4–1.7	3–4
	Coprosma petriei	No	Translucent pale blue	3.5–5.8 × 2.5–5.5	Pyrenes within a fleshy drupe	1.8–3(–3.4) × 1.5–2.1	(1–)2(–4)
	Coprosma propinqua	Yes	Blue, purple, white, yellow	3–5 × 4–6	Pyrenes within a fleshy drupe	4–5.5(6.3) × 3–4	(1–)2(–4)
	Coprosma rugosa	No	White, blue flecks	6–8	Pyrenes within a fleshy drupe	2.8–4.2 × 1.8–2.4	(1–)2(–4)
	Coprosma serrulata	No	Red–orange	7 × 9	Pyrenes within a fleshy drupe	5–6.5 (–7) × 3–4.1	(1–)2(–4)
	Nertera balfouriana	No	Yellow to orange	5–10	Pyrenes within a fleshy drupe	1.5–2.4	(1–)2(–4)
Santalaceae	*Exocarpus bidwillii*	No	Red	6–9(–9.5)	Nut in enlarged fleshy pedicel	4.5–6(–6.5)	1
Thymeliaceae	*Pimelea oreophilla*	Yes	Red, orange	4 × 3	Single-seeded drupe	2.1–3.5	1
	Pimelea sericeovillosa	No	Brown–orange	4 × 3	Single-seeded drupe	2–2.5	1
Violaceae	*Melicytus alpinus*	Yes	White, flecked, purple	3–6 × 5–8	Berry	3.8–4.4	1–2

[a] Seed dimensions and seed numbers taken from Webb, C.J. and Simpson M.J.A, 2001. Seeds of New Zealand Gymnosperms and Dicotyledons. Manuka Press, New Zealand.

[b] *Astelia linearis* dimensions from from C.J. Webb, unpublished data.

[c] *Coprosma* fruit dimensions taken from *Coprosma* key online Landcare Research, http://www.landcareresearch.co.nz/research/biosystematics/plants/coprosmakey/Coprosma.html.

Table A2
Summary of collective kea feeding activity using discrete individual feeding observations, separated by morning and evening observations, and by study site. Times are presented in minutes/s (±1 s.e. in seconds).

Site	Time	N feeding bouts	Feeding bout length, mean	Feeding bout length, range	Total feeding time
Red Tarns	AM	133	3:28 (0:19)	0:20 – 11:00	436:50
	PM	8	3:26 (0:18)	0:05 – 15:58	26:05
Sugarloaf	AM	16	0:44 (0:19)	0:02 – 2:30	12:07
	PM	72	2:46 (0:04)	0:02 – 15:30	177:35
Totals		229			652:37

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