

THE IMPORTANCE OF BIRDS AS BROWSERS, POLLINATORS AND SEED DISPERSERS IN NEW ZEALAND FORESTS

Summary: New Zealand's forest plants evolved in the absence of mammalian herbivores, but subject to the attentions of a variety of other animals. Insects are and probably were, the primary folivores, but birds may also have been important. Several extinct birds, notably moas (*Dinornithidae*), were herbivores, and speculation continues about their impact on the vegetation. Among existing forest birds, both kereru (*Hemiphaga novaeseelandiae*) and kokako (*Callaeas cinerea*) can significantly defoliate plants and may have had a greater impact in the past. Beneficial interactions of birds with forest plants include pollination and seed dispersal. Flower visitation by birds has already been reviewed, but the importance of frugivory and seed dispersal by birds has hitherto been given scant regard in New Zealand. About 70% of the woody plants in New Zealand forests have fruits suited for vertebrate dispersal and, of these, most are probably dispersed by birds. The recent extinction of several frugivorous forest birds (e.g., moas, piopio *Turnagra capensis*, huia *Heterolocha acutirostris*) and the decline of others (e.g., kokako) has reduced the number of potential seed dispersers, especially for large-fruited species, some of which now depend almost entirely on kereru for seed dispersal. A similar recent loss of potential seed dispersers has occurred throughout Polynesia, but consequent effects on patterns of forest regeneration are unknown.

Keywords: Browsing, pollination, frugivory, birds, forest, seed dispersal.

Introduction

Interest in the relationships between birds and plants in New Zealand has been stimulated by the realisation that extinct moas (*Dinornithidae*) were forest-dwelling browsers and frugivores (Duff, 1966; Gregg, 1972; Burrows, 1980; Burrows *et al.*, 1981). This means that, contrary to the earlier view that introduced mammals entered and devastated a naturally unbrowsed vegetation (Howard, 1965), the New Zealand flora evolved in the presence of at least some vertebrate browsing pressure.

In this paper we emphasise the point that, in addition to moas, other bird species may have been (and in some cases still are) significant browsers of forest vegetation. We also review the potential importance of flower visitation and frugivory by birds and note that New Zealand now has very few potential dispersers of large-fruited forest plants, following the recent extinction or decline of several frugivorous species.

Browsing

The most widespread, abundant and important browsers of vegetation in New Zealand forests are invertebrates. Trees can be almost totally defoliated by them over wide geographic areas. Examples of such damage are browsing of red beech (*Nothofagus fusca*)* by the beech leafroller, *Epichorista emphanes* and of mountain beech (*N. solandri*) by the mountain

beech moth, *Proteodes camilex*. The more usual impact of invertebrate browsing is not so spectacular; rather it is a persistent but important influence on the development of plants.

The other major browsers in the forests which covered most of prehistoric New Zealand (> 1000 yrs BP) were birds. Recent speculation about the importance of browsing by birds has concentrated almost exclusively on the possible impact of moas (Greenwood and Atkinson, 1977; Lowry, 1980; Atkinson and Greenwood, 1980), which were flightless and therefore capable of browsing only the understorey plants. The possible impact of other browsing birds, especially flying or climbing species capable of feeding at all levels in the forest, has been virtually ignored. At least five species of non-ratite forest birds eat significant quantities of foliage (Table 1), including the leaves of several species known to have been browsed by moas (Burrows *et al.*, 1981). Prominent among these forest browsers are the kereru, or New Zealand pigeon (*Hemiphaga novaeseelandiae*), and the kokako (*Callaeas cinerea*), both of which feed at all levels in the forest and are capable of significantly defoliating their favoured food plants. We will concentrate on these two species in more detail.

*Botanical names follow Allan (1961) with recent changes according to the list of Norton (1986).

Kereru

Kereru have been observed eating the leaves of 41 species of native plants (Table 1) and over 20 introduced species (McEwen, 1978, pers. obs.). Despite this wide range of recorded foods, they are in fact quite selective browsers within native forests and concentrate mainly on the old leaves of *Sophora*, *Parsonsia* and *Coprosma* spp. (Clout *et al.*, 1986; and pers. obs.). Other native plants which are regularly browsed (pers. obs.) include *Paratrophis microphylla*, *Melicytus micranthus*, *Hoheria* spp. and *Plagianthus regius* (from which both leaves and young twigs are taken). Foliage of all kinds is eaten mainly in late winter, spring and early summer, when fruit is least available. At these times of year, kereru are almost entirely folivorous and congregate in lowland habitats, especially along river valleys, where favoured foliage foods occur. Individual birds tend to become sedentary and, especially when feeding on *Sophora*, may concentrate their feeding activity in just a few trees for several weeks (Clout *et al.*, 1986). Although kereru usually feed for less than two hours per day when on a leaf diet (pers. obs.), the concentration of this activity on just a few individual plants can lead to quite intense browsing pressure. Observed feeding rates indicate that in 100 minutes of feeding, spread over a whole day, an individual kereru could eat 2300 leaflets of *Sophora microphylla*, or 2050 leaves of *Coprosma areolata*, or 1200 leaves of *Parsonsia heterophylla*. In practice, birds usually divide their feeding between two or more types of foliage in a day, although in individual foraging bouts they often concentrate on one species.

This sort of browsing pressure, which is commonly sustained for several weeks, can result in noticeable defoliation of favoured plants. Kereru can severely defoliate introduced deciduous trees. For example, flocks of up to 50 of them have been seen

browsing on the young leaves of elms (*Ulmus carpinifolia*) growing in a small copse near the Pelorus Bridge Scenic Reserve in Marlborough. In December 1984 individual birds were taking an average of 865 'beakfuls' of elm foliage per day. Assuming conservatively that 'beakfuls' averaged 2 cm², the kereru feeding in this copse would have eaten 268 m² of elm foliage in one month. Kereru browsing left the trees in a very ragged state.

Crop contents also illustrate the quantities of foliage consumed by kereru. The crop of a bird which was killed by a stoat at Lake Rotoroa in October 1984 contained c. 260 leaves of *Parsonsia heterophylla* (178 of them complete, and measuring up to 7 cm long), with a total dry weight of 5.4 g. McEwen (1978) found 14.2 g dry weight of leaves (mainly *Sophora tetraptera*) in the crop of one of the kereru which she dissected.

Although kereru are still widespread and moderately common, they were undoubtedly much more abundant in pre-European and prehistoric times, before the lowland forests (their main habitat) were cleared and predators were introduced. The browsing pressure of kereru congregating on riversides and lakeshores in winter and spring to feed on leaves of *Sophora*, *Plagianthus* and other favoured plants was probably much more intense than we see today. In the debate about the role of browsing by moas in the evolution of the New Zealand flora (Greenwood and Atkinson, 1977; Lowry, 1980; Atkinson and Greenwood, 1980), the possible influence of browsing by kereru in canopy, subcanopy and understorey should not be ignored. The phenology (e.g., deciduous habit), morphology (divarication, small leaves) and leaf chemistry (secondary compounds) of favoured food plants are as likely to have responded to selection pressures caused by heavy seasonal browsing by kereru as to browsing by moas.

Table 1: *Folivorous birds in New Zealand forests.*

Bird species	Plants eaten	Reference
Moa (12 spp.)	Gymnosperms 4 spp., Dicots 13 spp., Monocots 2 spp.	Burrows <i>et al.</i> 1981.
Kereru	Ferns 4 spp., Gymnosperms 1 sp., Dicots 36 spp.	McEwen 1978, pers. obs.
Kokako	Mosses, Ferns > 10 spp., Gymnosperms 4 spp., Dicots 30 spp., Monocots 3 spp	Hay 1981
Kakapo	Mosses and liverworts, Ferns 13 spp., Gymnosperms 5 spp., Dicots 35 spp, Monocots 32 spp.	Best 1984, R.G. Powlesland pers. comm.
Red-crowned parakeet	Dicots 13 spp., Monocots 1 sp.	Dawe 1979.
Yellow-crowned parakeet	'Wide range'	Taylor 1985

Kokako

In the central North Island, Hay (1981) found that kokako took leaf material from about 50 plant species (Table 1). Foliage comprised 30% of their total diet, measured as percentage of time spent feeding. Important species (those comprising more than 10% of the diet in anyone season) included moss, houndstongue fern (*Phymatosorus diversifolium*), *Asplenium flaccidum*, *Prumnopitys taxifolia*, *Dacrydium cupressinum*, *Pennantia corymbosa*, epiphytic orchids, *Muehlenbeckia*, *Tetrapathaea tetrandra*, *Melicytus ramiflorus*, *Hedycarya arborea* and *Laurelia novaezelandiae*.

The effects of kokako browse may not be as obvious as those of kereru, but one of the kokako's most important food items, the sixpenny scale insect (*Ctenochiton viridis*), is gleaned in such a way that the host plant is defoliated. The sixpenny scale adheres to the undersides of leaves of a variety of tree species (P. Maddison, pers. comm.) and is abundant on pate (*Schefflera digitata*) and broadleaf (*Griselinia littoralis*) at Pureora Forest. Kokako remove leaves, then carry them to a perch where they systematically pick the scale insects off. In one typical 20-minute feeding bout at Pureora, a pair of kokako removed 60 compound pate leaves from a single tree. During that season (summer 1978-79) scales on pate comprised a mean 24.6% of kokako food in the Pureora study area, while in spring 1980, scales on broadleaf comprised 77.4% of the diet (recorded as percentage of total feeding observations). The effects of this feeding on host trees may be profound, as shown by the litter of discarded leaves following a feeding bout. This resembles that left by possums (*Trichosurus vulpecula*) after they have fed on *Pseudopanax arboreum* petioles.

Kokako were previously abundant in both the North and South Islands, and may have had a significant impact as browsers of forest vegetation.

Pollination

Godley (1979) and Lloyd (1985) reviewed the floral biology and pollination of New Zealand plants and both concluded that New Zealand has relatively few specialised pollinators. Insects are by far the most common flower visitors, but there are over 30 plant species whose flowers are visited by birds (Godley, 1979; Craig *et al.*, 1981). Only about half of the plants concerned are clearly adapted to bird pollination (Lloyd, 1985), notably *Fuchsia*, *Sophora* and *Phormium*, which have large tube-like flowers

and are commonly visited by nectar-feeding birds such as bellbird (*Anthornis melanura*) and tui (*Prosthemadera novaezelandiae*). Birds may be important pollinators for these and a few other plants, but for the New Zealand flora as a whole they are relatively unimportant compared with Australia or central American forests (Lloyd, 1985).

Birds which visit (and potentially pollinate) the flowers of forest plants in New Zealand are the bellbird, tui, stitchbird (*Notiomystis cincta*), kaka (*Nestor meridionalis*), red-crowned parakeet (*Cyanoramphus novaezelandiae*), yellow-crowned parakeet (*C. auriceps*), saddleback (*Philesturnus carunculatus*) and silvereye (*Zosterops lateralis*) (Godley, 1979). This is a relatively small suite of flower-visiting birds (Ford *et al.*, 1979). Throughout most of the mainland forests of New Zealand, the only birds which commonly visit flowers are bellbird, tui and silvereye, because stitchbird and saddleback are extinct on the main islands and kaka and parakeets occur only in large tracts of forest.

Despite this, it is unlikely that any New Zealand plant is threatened by a lack of specialised bird pollinators. Few, if any, plants are exclusively pollinated by birds and there is no evidence of tight coevolution between particular bird species and particular flowers. For example, the flowers of *Sophora* (a tree which is commonly regarded as being pollinated by honeyeaters) are visited by at least four bird species, as well as bees, butterflies and moths. As further evidence of non-specialisation, the species *S. microphylla* occurs not only in New Zealand, but also Chile, where it is visited by hummingbirds and large bumble bees (Godley, 1979).

Godley (1979) considered that, although a diversity of flower types is visited by birds in New Zealand, most are visited 'incidentally' and the advantage to the plant is unclear, since birds may foster self-pollination more than anything else, especially in plants with monomorphic flowers. He stressed that more attention should be given to the end result of pollination, i.e., the percentage of ovules which produce seeds. Until such research is carried out, the importance of birds as pollinators in New Zealand forests remains uncertain.

Frugivory and Seed Dispersal

Most species of New Zealand forest bird are known to include some fruit in their diet. Even primarily insectivorous species such as grey warbler (*Gerygone igata*), fantail (*Rhipidura fuliginosa*) and pied tit

(*Petroica macrocephala*) will occasionally take small fruits (Moed and Fitzgerald, 1982). This is, perhaps, a result of the broad individual niches of the species in our relatively depauperate avifauna. Among the birds which eat fruits regularly are the parrots - kea (*Nestor notabilis*), kaka, kakapo (*Strigops habroptilus*), red-crowned parakeet and yellow-crowned parakeet. These species chew and crack larger seeds with their relatively powerful bills and so must be regarded primarily as seed predators. However, some small seeds are dispersed (e.g. *Coprosma pseudocuneata* by kea (Clarke, 1970), and *Cyathodes juniperina* by kakapo (Best, 1984). Kaka are known to destroy both green and ripe seeds of miro (*Prumnopitys ferruginea*) and matai (*P. taxifolia*) (A.E. Beveridge, pers. comm.; Beveridge, 1964).

Among the known frugivores which could have acted as seed dispersers in prehistoric New Zealand are several species which are now extinct (Table 2). These include moas, which ate the fruits or seeds of various plants, including trees such as matai, pokaka (*Elaeocarpus hookerianus*) and putaputaweta (*Carpodetus serratus*) (Burrows *et al.*, 1981). The extent to which moas could have acted as seed dispersers is uncertain, but they may have been important for dispersal of fallen fruit, perhaps performing a similar role to that of cassowaries (*Casuaris casuaris*) in North Queensland rainforests (Stocker and Irvine 1983). Thin-coated seeds (e.g. *Beilschmiedia* spp.) may have been crushed and ground by the stones in moa gizzards, but it is likely that the woody seeds of species such as *Vitex lucens*,

Table 2: Seed dispersing birds. in New Zealand forests.

Weight (g)	Common name	Scientific name	Gape (cm)**
> 5000	Moa	<i>Dinornithidae</i> (12 spp.)	>5.0
500-5000	(Brown kiwi)	<i>Apteryx australis</i>	2.4
	[Little spotted kiwi]	<i>Apteryx oweni</i>	2.1
	(Weka)	<i>Gallirallus australis</i>	1.3
	Kereru	<i>Hemiphaga novaeseelandiae</i>	1.4
	[Huia]	<i>Heteralocha acutirostris</i>	1.5
	(Kokako)	<i>Callaeas cinerea</i>	1.3
	Tui	<i>Prothemadera novaeseelandiae</i>	0.9
	[Piopio]	<i>Turnagra capensis</i>	1.1
	[Saddleback]	<i>Philesturnus carunculatus</i>	0.8
	50-500	+ Blackbird	<i>Turdus merula</i>
+ Song thrush		<i>Turdus philomelos</i>	1.0
+ (Indian myna)		<i>Acridotheres tristis</i>	0.9
+ (Starling)		<i>Sturnus vulgaris</i>	0.9
[Stitchbird]		<i>Notiomystis cincta</i>	0.7
Bellbird		<i>Anthornis melanura</i>	0.6
(NZ Robin)		<i>Petroica australis</i>	0.5
(Yellowhead)		<i>Mohoua ochrocephala</i>	>0.5
(Whitehead)		<i>Mohoua albicilla</i>	>0.5
>50		Silvereye	<i>Zosterops lateralis</i>
	(Brown creeper)	<i>Finchsia novaeseelandiae</i>	>0.5
	(Pied tit)	<i>Petroica macrocephala</i>	>0.5
	(Fantail)	<i>Rhipidura fuliginosa</i>	>0.5
	(Grey warbler)	<i>Gerygone igata</i>	>0.5
	(Rifleman)	<i>Acanthisitta chloris</i>	>0.5

* Parrots (Psitticidae) are classed as primarily seed predators, although they disperse some small seeds. Other species such as rock wren (*Xenicus gilviventris*) (pers. obs.) and gulls (*Larus* spp.) (Campbell 1967) eat some fruit but are not forest dwellers.

** Mean external distance between commissural points, measured on museum specimens. This is only a rough index of bill capacity; for example kereru have a distensible gape and can swallow fruit up to 2.5 cm in diameter (Gibb 1970).

- Square Bracketed – species extinct on mainland New Zealand.
 Round Bracketed – minor frugivore and/or a species with restricted distribution.
 Bold type – major frugivore, widely distributed.
 + – introduced species.

Prumnopitys and *Elaeocarpus* spp. could have passed intact (albeit somewhat abraded) through the digestive tract of a moa. Such abrasion might conceivably enhance the germination prospects of woody seeds, but there is no evidence of extreme coevolution of such seeds for dispersal by moas, such as may have occurred with the seeds of *Calvaria major* for dispersal by dodo (*Raphus cucullatus*) on Mauritius (Temple, 1977). Brown kiwi (*Apteryx australis*) also take woody seeds, including miro, hinau (*Elaeocarpus dentatus*) (Buller, 1888) and nikau (*Rhopalostylis sapida*) (Simpson, 1971) and may use these as substitute gizzard stones.

The range of fruits eaten by extinct species such as huia (*Heteralocha acutirostris*) and piopio (*Turnagra capensis*) is even more difficult to establish than for moas (which have left subfossil gizzard contents). Buller (1888) reported that huia ate fruits of hinau, pigeon wood (*Hedycarya arborea*) and *Coprosma* sp. and piopio are known to have eaten *Fuchsia* fruit. It is likely that both species ate a wide range of fruits, but unfortunately their diet was never properly recorded.

The importance of birds as dispersers of the seeds of New Zealand forest plants must not be underestimated. Of the c. 240 species of woody plants occurring in New Zealand's mainland forests, about 70% have fleshy fruits suited for vertebrate dispersal. Some of these species may have evolved primarily for dispersal by lizards (A.H. Whitaker, pers. comm.) but

the majority (especially the orange, red and black fruits) are undoubtedly dispersed by birds. The extinction or decline of several bird species in the past few hundred years has reduced the number of effective dispersers, especially for plants with large fruits (> 1cm diameter) (Table 3). For these plants; kereru are now virtually the sole dispersers. Overall, kereru eat the fruits of at least 70 species of plants (P. E. Cowan and M.N. Clout unpub.). They are arguably the most important seed-dispersing birds in New Zealand forests, because of their catholic diet, their mobility, and their widespread distribution.

An example of the quantity of fruit consumed by kereru is provided by the intensive radio-tracking of one bird in the Pelorus Bridge Scenic Reserve, Marlborough. During the miro fruiting season of 1984 (April-July inclusive) kereru 'G' spent 87% of its feeding time taking miro fruit. It fed in 17 different miro trees, but 82% of its miro feeding was concentrated in one tree, which it successfully defended against other birds. The number of fruits it removed from this tree was calculated as 97.7 per day, or a total of 9816 over the four months. By mid-August no fruits were left on the tree but 1662 uneaten ones were counted beneath it. Assuming no fruits were taken by other animals, the estimated total crop was 11478, of which kereru 'G' took 85%.

For kokako in the central North Island, fruit comprised over 80% of the diet in summer and autumn of 1981 (Hay 1981). Fruits much larger than

Table 3: Known dispersers of large fruits.

Fruit Diameter (cm)	Plant species	Brown Kiwi	Weka	Kereru	Kokako	Tui	Blackbird	Song Thrush
>1.4	<i>Corynocarpus laevigatus</i>			*				
	<i>Vitex lucens</i>			*				
	<i>Beilschmiedia tarairi</i>			*				
	<i>Beilschmiedia tawa</i>			*				
	<i>Beilschmiedia tawaroa</i>			*				
	<i>Planchonella costata</i>			*				
>1.0	<i>Prumnopitys ferruginea</i>	*	*	*	*		*	
	<i>Syzygium maire</i>			*				
	<i>Dysoxylum spectabile</i>		*	*	*			
	<i>Litsea calicaris</i>			*	*			
	<i>Elaeocarpus dentatus</i>	*	*	*	*			
	<i>Ripogonum scandens</i>			*	*	*	*	*
>0.6	<i>Hedycarya arborea</i>		*	*	*	*	*	*
	<i>Nestegis cunninghamii</i>			*	*	*	*	*
	<i>Rhopalostylis sapida</i>	*		*	*	*	*	*
	<i>Alectryon excelsus</i>			*	*	*	*	*
	<i>Prumnopitys taxifolia</i>		*	*	*	*	*	*

Asterisks show known dispersers of each plant.

Brown kiwi, weka and kokako have restricted distributions and so are not major dispersers.

1 cm in diameter were not eaten whole but had the pericarp stripped off, while smaller fruits from species such as supplejack (*Ripogonum scandens*) and pigeonwood, were usually swallowed whole. In one season at Mapara, King Country, the seeds from a crop of unusually large supplejack fruits were discarded after pericarp stripping instead of whole fruits being swallowed (Hay 1981).

Kokako eat the fruit of at least 35 species (J.R. Hay, unpubl.) and may once have been almost as important for seed dispersal as kereru. However, they are not potentially long-distance seed dispersers like kereru, because they are weak fliers and inhabit permanent territories of less than 11 ha. Unfortunately kokako are now rare and restricted to only a few North Island forests.

Conclusions

This review of interactions between birds and plants in New Zealand forests has illustrated the previous diversity and importance of these interactions (especially browsing and seed dispersal) and the extent to which they have been disrupted and diminished by recent bird extinctions.

We conclude that not only moas (Greenwood and Atkinson 1977), but also canopy-feeding birds such as kereru and kokako exerted significant browsing pressure on some plants in the prehistoric forests of New Zealand. Because of extensive dietary overlap between different herbivorous birds and the turnover of both bird and plant species through evolutionary time, it is unlikely that particular plant species have evolved adaptations to browsing by particular birds, although evolutionary responses to bird browsing in general are possible. With the extinction of moas and the recent decline of other birds such as kokako and kakapo, browsing by birds no longer has a great impact on forest plants, although kereru are still capable of significant local defoliation.

Birds perform a relatively minor role as pollinators in New Zealand forests (Godley 1979), and it is unlikely that they were significantly more important in the past, even when stitchbirds were present on the mainland and other flower visitors such as kaka were more abundant.

The most important bird-plant interactions in New Zealand forests today (and probably also the most important in prehistoric forests) are those hinging on avian frugivory and seed dispersal. About 70% of New Zealand's forest bird species (including most small insectivores) eat fruits. Most New Zealand fruits are clearly adapted for bird dispersal, although

more information is needed on which ones are eaten by which birds. It appears, however, that most fruits are (and presumably always were) eaten and dispersed by several different bird species (P.E. Cowan and M.N. Clout unpubl.). Tight coevolution between particular fruiting plants and particular frugivorous birds is therefore unlikely to have occurred (Herrera 1985).

Because of the spate of recent extinctions of frugivorous birds (e.g., moas, huia, piopio), and the diminished range of others (e.g., kiwis, kokako, weka (*Gallirallus australis*)), New Zealand now has a relatively small number of effective seed dispersers, especially for large-fruited plants. Several of these now depend almost entirely on kereru for their dispersal. This is a precarious situation, especially where kereru are either rare, as on the Chatham Islands, or recently extinct, as on Raoul Island.

A depleted avifauna is a feature not only of New Zealand, but also of other island groups in Polynesia, where many birds (including several known or probable frugivores) have become extinct following human settlement (Olson and James 1982, Cassels 1984, Steadman 1985, Steadman and Olson 1985). The disruption of ecological processes, such as seed dispersal and forest regeneration, in the wake of these extinctions may have been considerable and this is a subject worthy of closer study.

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