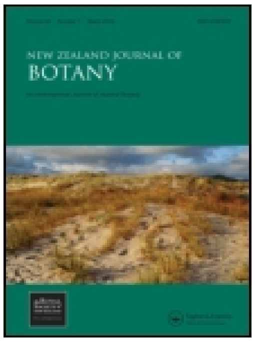

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The roles of lizards in New Zealand plant reproductive strategies

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Abstract Geckos in the genus *Hoplodactylus* regularly visit flowers to feed on nectar. They collect considerable amounts of pollen, mostly on their throats, from species such as *Metrosideros excelsa* and *Phormium tenax*. This pollen can be carried for many metres and for up to at least 12 hours, and there is thus the opportunity for lizards to transfer it to a conspecific plant to effect cross-pollination.

Geckos in the genus *Hoplodactylus* and skinks in the genera *Leiolopisma* and *Cyclodina* all include considerable quantities of fleshy fruit in their diet during summer. Fruits most commonly consumed are in the genera *Coprosma, Gaultheria, Hymenanthera, Macropiper,* and *Muehlenbeckia*. Seeds pass through the gut undamaged and germination trials showed that at least some are viable. Because of the size, colour, and positioning of the fruit it appears that some divaricating shrubs (e.g., *Coprosma, Hymenanthera*) or vines (e.g., *Muehlenbeckia*) may be specifically adapted to seed dispersal by lizards.

Keywords pollination; seed dispersal; nectarivory; frugivory; lizard; gecko; skink

INTRODUCTION

There are two stages in the reproductive cycle of a plant when lizards could play a beneficial role — during pollination and during seed dispersal. Zoophily (animal-mediated pollination) has traditionally been considered the domain of nectarivorous invertebrates (usually insects), birds and, to a lesser extent, mammals (Gilbert & Raven 1975; Armstrong 1979; Faegri & Pijl 1980; Bentley & Elias 1983; Real 1983; Janzen 1985) and this is certainly the situation in New Zealand (Heine 1937; Godley 1979; Lloyd 1985); zoochory (animal-mediated seed dispersal) is generally by birds, mammals or rarely reptiles (Gilbert & Raven 1975; Pijl 1982; Janzen 1985) but in New Zealand it has always been assumed that seeds from fleshy fruits are distributed by birds (Beveridge 1964; Simpson 1971; McEwen 1978; Lloyd 1985; Webb 1985).

Nectarivory and the consumption of other plant exudates has been recorded for several lizard species, mostly geckos (Whitaker 1968; Vinson & Vinson 1969; Vinson 1975; Elvers 1977, 1978; Thorpe & Crawford 1979; Cogger et al. 1983; Cheke 1984). The predilection of captive New Zealand geckos for sugar-water or honey has led to suggestions that in the wild they might eat nectar (McCann 1955; Rowlands 1981) but only two observations of nectarivory by New Zealand species have been documented (Whitaker 1968; Miller 1986). Robb (1973, 1986) recognised that nectarivory by New Zealand geckos could result in some pollination of forest plants but implied (1986:12) it was accidental and regarded it as "insignificant". Only Elvers (1977, 1978) has proposed that lizards should be seriously considered as pollinators.

Frugivory is relatively common amongst lizards and some lizards are regarded as seed-dispersers (Borzi 1911; Racine & Downhower 1974; Barquin & Wildpret 1975; Symon 1979; Clifford & Hamley 1982; Pijl 1982; Iverson 1985). Many New Zealand lizards have long been known to include berries or other soft fruit in their diet (Sladden & Falla 1928; McCann 1955; Bull & Whitaker 1975; Whitaker 1976; Gill 1986; Robb 1986).

This paper summarises the observations of nectarivory and frugivory by lizards from New Zealand and proposes that the role played by lizards in the reproductive strategies of some plants may be far more significant than previously recognised. A concurrent article has colour illustrations of lizards feeding on nectar and fruit (Whitaker 1987).

LIZARDS AS POTENTIAL POLLINATORS

Hoplodactylus duvauceli has been seen taking nectar from pohutukawa (*Metrosideros excelsa:* Myrtaceae), ngaio (*Myoporum laetum:* Myoporaceae) and flax (*Phormium tenax:* Agavaceae), and *Hoplodactylus pacificus* has been seen feeding on nectar

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from pohutukawa, ngaio, flax, and *Hebe bollonsii* (Scrophulariaceae). *H. pacificus* has also been found foraging on the flowers of ti (*Cordyline australis:* Agavaceae) and *Sicyos angulata* (Cucurbitaceae) but was not actually seen taking nectar. *Hoplodactylus granulatus* has been reported feeding from rata flowers (*Metrosideros ?umbellata:* Myrtaceae) (A. Terrill pers. comm. to B. W. Thomas). These three geckos are nocturnal and are agile climbers. The diurnal, arboreal gecko *Naultinus grayi* has been seen feeding on manuka nectar (*Leptospermum scoparium:* Myrtaceae) (M. Bellingham pers. comm.).

New Zealand geckos have most often been seen feeding on pohutukawa nectar. Flowers on pohutukawa trees open sequentially with individual flowers lasting 6–8 days. Inflorescences have flowers open for up to 12 days, and flowering may take place over six weeks (Godley 1978). Similarly, individual trees within a population flower at different times over a season lasting 6–10 weeks (Godley 1978).

When pohutukawa blooms, geckos (*H. duvauceli* and *H. pacificus*) preferentially congregate on flowering plants to feed on nectar. Whitaker (1968) reported over 50 *H. pacificus* on the flowers of a small, isolated pohutukawa which had a canopy surface of approximately 21 m^2. Allowing for approximately 50% of the canopy surface to be covered in flowers (pohutukawa flowers only on the canopy), there were nearly 5 geckos m^{-2} of flowers feeding on this tree. On Aorangi Island, Poor Knights group, two small pohutukawa trees, adjoining an area of larger pohutukawas, were observed to have 7–8 geckos m^{-2} of flowers on most nights over a three week period in November 1984.

Geckos group around the newly opened flowers, presumably because these have the greatest nectar production, and up to five geckos have been seen feeding together from a single inflorescence. Density of geckos m^{-2} flowers at the right stage for pollination is therefore probably higher than the above figures indicate.

The geckos emerge at dusk, usually from retreats on the ground, and can often be seen on the flowers before it is dark. This is earlier than usual and suggests there may be competition for the nectar. The greatest foraging activity for nectar is in the first 2–4 hours after dusk. When foraging, the geckos climb over the surface of the flowers and push their heads down between the stamens to lap the nectar (Fig. 1; see also Whitaker 1987), usually working from one flower to the next across the inflorescence. They then move through the foliage in search of another inflorescence.

Ngaio flowers are much smaller and more scattered than those of pohutukawa but are nonetheless keenly sought by *H. pacificus;* only once has *H. duvauceli* been seen feeding on ngaio nectar. Geckos forage amongst the foliage or along the stems of ngaio until a flower is located. They then arch their necks to push the snout well down into the flower to reach the nectar. On Aorangi Island in November 1984 each ngaio bush along the shore generally had 2–4 geckos each night feeding on nectar.

The flowers of flax are so robust that only *H. duvauceli* or adult *H. pacificus* are able to force the petals apart to reach the nectar. They push their snout into the open end of the flower, prise the petals apart along one side and lap the nectar through the side of the flower (similar behaviour was reported for *Phelsuma vinsoni* feeding on the nectar of *Lomatophyllum* sp. (Liliaceae) (Vinson & Vinson 1969)). Smaller geckos forage over the flax inflorescences searching for scattered droplets of nectar, damaged flowers or other accessible nectar sources. Densities of lizards taking flax nectar are not easy to calculate but Miller (1986) reported 1–6 *H. pacificus* (usually 4–6) feeding on ***each*** flax inflorescence on Whale Island, Moturoa group, in November 1985. Three *H. pacificus* were observed feeding on nectar from flowers on one bract of a flax inflorescence on Green Island, Mercury group, in November 1972.

There has been only one observation of a gecko feeding on *Hebe bollonsii* flowers; an adult *H. pacificus* was seen clinging to the erect inflorescence and lapping nectar from each flower in turn.

Geckos have also been seen feeding on the fluid draining from wounds on the trunks of trees, and on honey-dew. On Little Ohena Island, east of Whitianga, over 80 *H. pacificus* were counted feeding on honey-dew on a 6 m tall karo *Pittosporum crassifolium:* Pittosporaceae) in November 1972.

To examine the potential for pollen dispersal, smears were collected from 32 geckos (15 *H. duvauceli* and 17 *H. pacificus*) on Aorangi Island in November 1984. At the time the samples were collected pohutukawa and ngaio were in full flower but other possible nectar sources (flax; ti; *Sicyos angulata;* puriri (*Vitex lucens:* Verbenaceae); *Xeronema callistemon* (Liliaceae)) had virtually finished flowering. Pollen smears were collected from geckos by pressing transparent adhesive tape ("Sellotape") to the undersurface of the throat and then sticking it to a glass microscope slide. These were examined at 100× magnification and identified by comparing the pollen with reference slides made from all the species in flower at the time of the survey. The amount of pollen was scored on an arbitrary scale based on that used by Gaze & Fitzgerald (1982) where:

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Fig. 1 *Hoplodactylus pacificus* feeding on the nectar from the flowers of pohutukawa (*Metrosideros excelsa*: Myrtaceae). Note how the bodies of the geckos are draped over the brush-structure of the inflorescence and the undersurface, especially the throat, is pressed against both stamens and stigmas.

0 = no pollen present
1 = very few pollen grains present
2 = scatter of single grains or a few small groups
3 = scattered groups of grains
4 = pollen always visible in field of view
5 = continuous scatter of pollen across the slide

The geckos sampled included three captured while feeding from pohutukawa flowers and one feeding from ngaio; these samples were used as a measure of pollen quantity carried close to the source. The rest of the sample included 20 geckos actively foraging away from flowering trees and 8 geckos captured by day from retreats on the ground while they were inactive.

Twenty-two (68.7%) of the geckos were carrying at least some pohutukawa pollen (Table 1); only the gecko sampled while feeding on ngaio had ngaio pollen. No pollen from other species was found. One *H. duvauceli* carried huge numbers of fungal spores from two species of sooty mould of the type commonly found on tree-trunks (A. E. Bell pers. comm.). Nearby, geckos were frequently observed feeding on exudate from bark-wounds, surrounded by sooty moulds, in several karo trees.

Five (62.5%) of the inactive geckos were carrying pohutukawa pollen. As these animals were sampled just before dusk, they must have been carrying pollen for at least 12 hours.

When geckos were sampled while actively foraging, no measure of the distance to the nearest nectar source was made because of the difficullty of doing so in forest at night. However, many of those which were carrying pohutukawa pollen were collected in an area 20–25 m from the nearest pohutukawa trees, and some animals with pohutukawa pollen were collected while foraging on the shore over 50 m from the nearest pohutukawa trees.

Geckos feeding on pohutukawa or flax nectar have visible amounts of pollen adhering to their heads, undersurface, and feet (see Whitaker 1987).

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Table 1 The occurrence of pohutukawa (*Metrosideros excelsa* : Myrtaceae) pollen on geckos on Aorangi Island, Poor Knights group, November 1984. See text for interpretation of pollen scores.

Hoplodactylus duvauceli (n = 15)

Pollen score	0	1	2	3	4	5	Total
Feeding on pohutukawa	0	0	0	0	0	1	1
Actively foraging	4	3	0	0	1	6	14
Inactive	0	0	0	0	0	0	0
Total	4	3	0	0	1	7	15
%	26.6	20.0	0	0	6.7	46.7	

Hoplodactylus pacificus (n = 17)

Pollen score	0	1	2	3	4	5	Total
Feeding on pohutukawa	0	0	2	0	0	0	2
Actively foraging	3*	2	0	1	0	1	7
Inactive	3	3	1	1	0	0	8
Total	6	5	3	2	0	1	17
%	35.3	29.4	17.6	11.8	0	5.9	

Total (all geckos)	10	8	3	2	1	8	32
%	31.3	25.0	9.4	6.3	3.1	25.0	

* includes one animal caught feeding on ngaio nectar which had a pollen score of 3 for ngaio.

Geckos examined while inactive, or foraging somewhere other than on plants from which they could collect nectar usually had pollen adhering only to their throats (see Whitaker 1987). Although nectar may stick the pollen to the skin of the gecko the behaviour of a feeding gecko shows the throat is probably the best region of the body for the transfer of pollen to the stigma. As the throat is the region of the body where most pollen adheres there is the possibility that other mechanisms of attachment are involved. Preliminary examinations with a scanning electron microscope of the skin of *H. pacificus,* the species most commonly observed feeding on nectar, have revealed interesting ultrastructural differences between the scales of the throat and those of other parts of the body (M. B. Thompson & A. H. Whitaker, in prep.).

LIZARDS AS POTENTIAL SEED DISPERSAL VECTORS

The first record of frugivory in New Zealand lizards was for *Lygosoma* (= *Leiolopisma*) *smithi* on the Alderman Islands where it was reported eating berries (Sladden & Falla 1928), later identified as taupata (*Coprosma repens:* Rubiaceae) (Falla 1936). However, despite the general acceptance now that both skinks and geckos commonly include fruit in their diet (McCann 1955; Bull & Whitaker 1975; Whitaker 1976; Gill 1986; Robb 1986), there have been relatively few observations of frugivory by New Zealand lizards. The lizards recorded taking fruit and the species they consume are listed in Table 2. The fruits of ngaio have not yet been recorded in the diet of New Zealand lizards but are taken by *Lacerta galloti* in the Canary Islands where ngaio is an introduced species (Barquin & Wildpret 1975).

Lizards observed feeding on fruit include nocturnal (*Hoplodactylus*) and diurnal (*Naultinus*) geckos, and nocturnal (*Cyclodina*) and diurnal (*Leiolopisma*) skinks.

The fruits taken are mostly drupes (*Coprosma, Corynocarpus, Leucopogon* (= *Cyathodes*), *Macropiper, Pimelea, Rubus*) but also include soft berries (*Hymenanthera, Solanum*) and other fleshy fruits (*Gaultheria, Muehlenbeckia*). Most are small, 3–6 mm in diameter, and are swallowed whole. Larger fruits such as kawakawa (*Macropiper excelsum:* Piperaceae), 8–10 mm diameter × 40–60 mm long, are eaten in pieces (Fig. 2). There is one record of a *H. duvauceli* eating a karaka (*Corynocarpus laevigatus:* Corynocarpaceae) fruit approximately 20 mm diameter × 30 mm long (see Whitaker 1987).

Geckos are extremely adept climbers and have no difficulty in reaching fruit. The skinks are largely

Table 2 Records of frugivory by New Zealand lizards. All observations are by the author unless otherwise indicated.

Lizard species	Plant species	Source
Family Gekkonidae		
Hoplodactylus duvauceli	*Corynocarpus laevigatus*	R.S. Slack, pers. comm.
	Coprosma sp.	I.C. Southey, pers. comm.
	Solanum nodiflorum	I.C. Southey, pers. comm.
	Macropiper excelsum	Whitaker 1968
	"seeds"	Barwick 1982
Hoplodactylus maculatus	*Coprosma propinqua*	
	Coprosma sp. (non *propinqua*)	
	Coprosma spp.	Whitaker 1982
	Hymenanthera alpina	
	Leucopogon fraseri	
	Muehlenbeckia axillaris	
	Muehlenbeckia [?complexa]	Whitaker 1982
	Rubus sp.	
	Solanum nodiflorum	I.C. Southey, pers. comm.
Hoplodactylus pacificus	*Macropiper excelsum*	Whitaker 1968
Naultinus grayi	*Cassytha paniculata*	M. Bellingham, pers. comm.
Family Scincidae		
Cyclodina alani	*Coprosma* sp.	Southey 1985
	Macropiper excelsum	Southey 1985
	Solanum nodiflorum	Southey 1985
Cyclodina oliveri	*Coprosma* sp.	Whitaker 1968
	Macropiper excelsum	Whitaker 1968
	Solanum nodiflorum	Southey 1985
Cyclodina whitakeri	*Macropiper excelsum*	Southey 1985
	Solanum nodiflorum	Southey 1985
Leiolopisma fallai	*Pimelea prostrata*	McCann 1955
Leiolopisma grande	*Coprosma ?propinqua*	
	Gaultheria ?antipoda	
	Hymenanthera alpina	
	Leucopogon fraseri	
	Muehlenbeckia axillaris	
Leiolopisma nigriplantare	*Gaultheria depressa*	Patterson 1985
	Hymenanthera alpina	
	Leucopogon fraseri	Patterson 1985
	"seeds" (2 spp.)	Barwick 1959
Leiolopisma otagense f. *otagense*	*Coprosma ?propinqua*	
	Coriaria ?sarmentosa	
	Gaultheria ?antipoda	
	Hymenanthera alpina	
	Leucopogon fraseri	
	Rubus sp.	Thomas 1982
	"seeds"	Thomas 1982
Leiolopisma otagense f. *waimatense*	*Coprosma ?propinqua*	Whitaker 1985
	Hymenanthera alpina	Whitaker 1985
	Muehlenbeckia axillaris	Whitaker 1985
Leiolopisma smithi	*Coprosma repens*	Falla 1936
	Macropiper excelsum	
	?Phytolacca octandra	Whitaker 1968
	Solanum nodiflorum	I.C. Southey, pers. comm.
	"berries"	Sladden & Falla 1928

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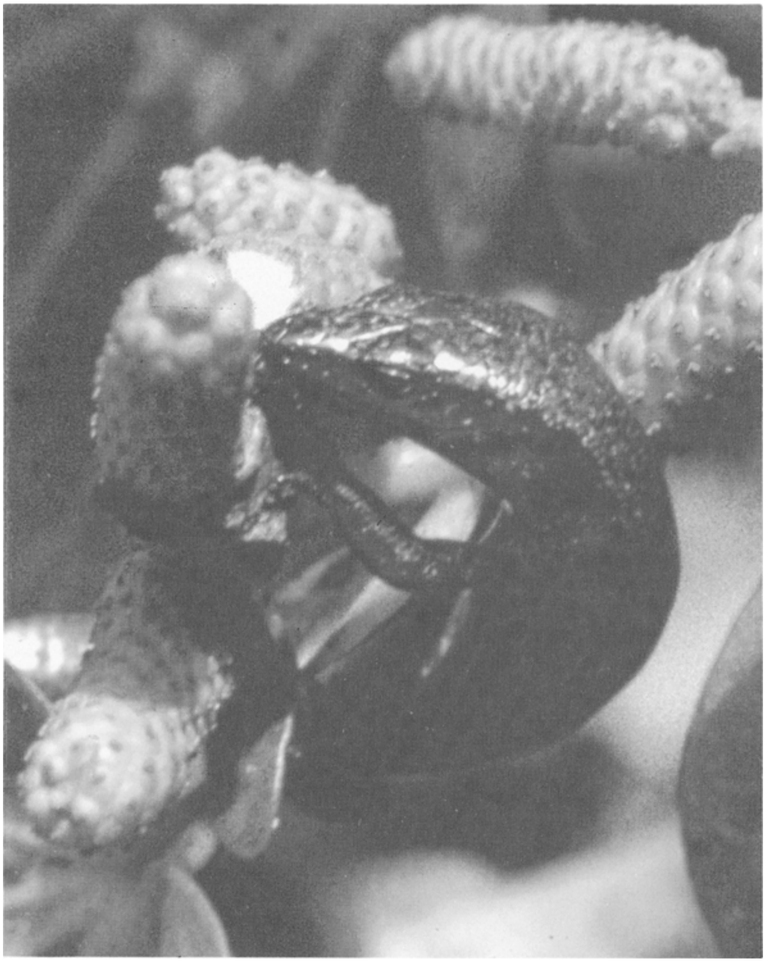

Fig. 2 *Leiolopisma smithi* feeding on ripe fruits of kawakawa (*Macropiper excelsum*: Piperaceae) over a metre above ground.

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terrestrial but can easily scramble through divaricating shrubs (*Coprosma, Hymenanthera*) or tangled vines (*Muehlenbeckia, Rubus*) and have been found several metres above the ground in such situations. On Green Island, Mercury group, *Leiolopisma smithi* individuals were observed climbing the smooth, vertical stems of kawakawa to reach fruits 1.5 m above the ground.

Small fruits are generally plucked from the plant as soon as they ripen and before they fall, although fruit that has fallen is readily consumed. At Macraes Flat, Otago, in March 1986, no ripe fruit was present on (or under) plants of *Hymenanthera alpina* (Violaceae), *Muehlenbeckia axillaris* (Polygonaceae), or *Gaultheria antipoda* (Ericaceae) on outcrops inhabited by *Leiolopisma grande* (and *L. grande* droppings were crammed with seeds of these species), yet plants on nearby outcrops without skinks were covered in ripe fruit. Similarly, on outcrops occupied by *Leiolopisma otagense* there were no ripe fruit on plants of *Hymenanthera alpina.*

Lizards seek out and consume only the ripe portions of larger fruits. The elongate fruit of kawakawa ripens from the top and lizards eat only the ripe part, moving round the plant to take the soft pulp as soon as it is edible. On the occasions when they encounter a fruit that is wholly ripe *L. smithi* have been seen to break the fruit from the plant and fall with it to the ground.

Most studies where New Zealand lizards were found to be eating fruit either do not include monthly samples or have not been analysed clearly to differentiate months (Barwick 1959, 1982; Whitaker 1982; Patterson 1985; Southey 1985), and the importance of fruit, assessed either by frequency of occurrence or by volume, is based on the whole sample. Because the fruits are available generally for only a short period in summer or early autumn,

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such studies invariably underestimate the seasonal importance of fruit in the diet of lizards.

Fruits of *Gaultheria depressa* (Ericaceae) and *Leucopogon fraseri* (Epacridaceae) are eaten by *Leiolopisma nigriplantare maccanni* and two unnamed sibling species in Central Otago tussock grasslands. Gut analyses on a sample collected over 21 months showed 4% (n=110) of *L. n. maccanni* contained berries which comprised 18% by volume of their diet; comparable figures for the other two taxa present were 3% (n=81) frequency and 15% volume, and 0.5% (n=210) frequency and 1% volume (Patterson 1985). Frequencies of fruit in the diet of those skinks containing food over the period that fruit was available were 4.4%, 3.6%, and 1.5% respectively (G. B. Patterson pers. comm.). Seeds (2 spp.) were recorded in 5.8% (n=68) of *Leiolopisma zelandica* (= *L. n. maccanni*) collected at various sites around Wellington over 19 months (Barwick 1959). Seeds of *Muehlenbeckia axillaris* and *Hymenanthera alpina* occurred in 86% (n=14) of fresh *Leiolopisma grande* droppings collected in February 1986 at Macraes Flat, Otago.

Diets of three large *Cyclodina* species on Middle Island, Mercury group, were compared by faecal analysis (Southey 1985): 6.9% of the droppings of *Cyclodina alani* (n=101) contained seeds of *Solanum nodiflorum* (Solanaceae), 8.9% contained seeds of kawakawa, and 0.9% contained seeds of *Coprosma* species; for *Cyclodina whitakeri* (n=89), 4.5% contained seeds of *S. nodiflorum*, and 3.4% contained seeds of kawakawa; and for *Cyclodina oliveri* (n=49), 4.0% contained seeds of *S. nodiflorum*. Fruit was an important component of the skinks diet over the period December to March when it comprised 31.5% of the diet of *C. alani* (n=54), 11.3% of the diet of *C. whitakeri* (n=62), and 8.7% of the diet of *C. oliveri* (n=23) (I. C. Southey pers. comm.). (Examination of 122 tuatara (*Sphenodon punctatus*) faecal pellets showed that 9.8% contained *Coprosma* seeds, 7.4% contained *Solanum nodiflorum* seeds, and 4.9% contained kawakawa seeds (I. C. Southey pers. comm.).)

At Turakirae Head, Wellington, fruit is seasonally important in the diet of *H. maculatus* (Whitaker 1982). The *H. maculatus* were collected monthly over a 12-month period and their diets determined from gut analyses. The seeds specifically identified were *Muehlenbeckia ?complexa* and *Coprosma propinqua*. *Muehlenbeckia* occurred only in the January and February samples; *Coprosma* was likewise most abundant in January and February but a few seeds were found from November to June. Over the whole sampling period 15.1% of the adult geckos which contained food (n=224) had eaten fruit but in January and February fruit was found in 65% and 50% of the animals, respectively (Table 3). The numbers of fruit eaten have been calculated by allowing one seed per fruit for *Muehlenbeckia* and two per fruit for *Coprosma*. The two *H. duvauceli* collected from The Brothers islands in Cook Strait which contained "seeds" (Barwick 1982) were presumably geckos from the summer sample (n=8).

DISCUSSION

These observations clearly show that some New Zealand lizards have the potential to be significant pollinators or seed dispersers for some species of New Zealand plants.

Pollination by lizards

To be effective, an animal pollinator must be a frequent and regular visitor to the flowers of a particular species, must be able to collect and carry pollen for long enough to distribute it to another

Table 3 Consumption of fruit by adult *Hoplodactylus maculatus* at Turakirae Head in January and February 1968 compared with the period May 1967 to April 1968.

	Jan	Feb	Total
No. adult lizards in sample	20	22	253
No. guts containing food	20	20	224
No. guts containing fruit	13	10	34
% guts with fruit	65.0	50.0	15.1
No. with *Muehlenbeckia* only	3	2	5
No. with *Coprosma* only	5	6	22
No. with *Muehlenbeckia* and *Coprosma*	5	2	7
Maximum no. *Muehlenbeckia* fruit/gut	14	5	14
Maximum no. *Coprosma* fruit/gut	7(−14)	5(−9)	7(−14)
Mean no. *Muehlenbeckia*/gut with *Muehlenbeckia*	4	3	3.7
Mean no. *Coprosma*/gut with *Coprosma*	2.1(−3.9)	2.25(−4)	1.7(−2.9)
Mean no. fruit/gut with fruit	4.1(−5.5)	3.0(−4.4)	2.8(−3.8)
Mean no. fruit/gut with food	2.7(−3.6)	1.5(−2.2)	0.4(−0.6)

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flower at the appropriate stage of maturity either on the same plant or on another of the same species, and must be able to deposit pollen on the stigma.

Hoplodactylus duvauceli and/or *H. pacificus* visit flowers of pohutukawa, ngaio, and flax in large numbers to feed on nectar. They visit them throughout the season, and forage actively from flower to flower, inflorescence to inflorescence, and probably from one plant to the next. Large amounts of pollen adhere to their bodies and they carry it for at least 12 hours and for up to 50 m from the source — a time and distance more than adequate to take it to other conspecific plants. The pollen is generally carried on the throat, which, especially for pohutukawa, is the best site for transfer to the stigma. What remains to be demonstrated is that lizards can, and do, transfer pollen from the anther to the stigma.

So far, in New Zealand, only the nocturnal, arboreal geckos in the genus *Hoplodactylus* have been commonly seen feeding on nectar but it is possible that other lizards do also. *Phelsuma* spp., geckos similar in size and behaviour to the diurnal arboreal geckos in New Zealand (*Naultinus, Heteropholis*), regularly take nectar (Vinson & Vinson 1969; Vinson 1975; Thorpe & Crawford 1979; Evans & Evans 1980; Cheke 1984) but here there are only three observations of *Naultinus grayi* feeding from manuka flowers (M. Bellingham pers. comm.). *Lacerta muralis dugesii*, a species on Madiera of similar size, form, and behaviour to many of the New Zealand *Leiolopisma* spp., has been observed taking nectar from several species of plants (Elvers 1977, 1978).

From the relatively few observations it is difficult to speculate on a floral syndrome for lizard-pollinated flowers. The reward for flower visiting by *Hoplodactylus* spp. appears to be nectar alone; geckos were only observed lapping nectar and none were seen eating pollen as is implied for *Phelsuma* spp. in the Seychelles Islands (Evans & Evans 1980; Cheke 1984) nor flowers as recorded for *Platydactylus* (=*Rhacodactylus*) *auriculatus* in New Caledonia (Bavay 1869). Flowers should therefore produce copious nectar and this is certainly true for pohutukawa and flax.

Lizards generally have a good sense of smell and good vision, including the ability to distinguish colours (Bellairs 1969). *Hoplodactylus* spp. certainly have an acute sense of smell and excellent eyesight (pers. obs.) but, as they are nocturnal, the level of their colour vision is perhaps less relevant. Scented flowers would therefore seem important but large, weakly-scented flowers such as pohutukawa or flax may be located visually as well as by odour. Red colouration of flowers is usually considered an ornithophilous character (e.g., Faegri & Pijl 1980) However, as red is invisible to most, if not all, pollinating insects, the red colour of many flowers may be a means of preventing nectar exploitation by diurnal insects, rather than as an attractant to birds, thus leaving most of the nectar for nocturnal pollinators (Raven 1972; Faegri & Pijl 1980). Perhaps the brilliant red of pohutukawa flowers has evolved so that most nectar is retained for nocturnal pollinators such as geckos. Knowledge of flower opening times and times of peak nectar production would help to determine whether the primary pollinator is nocturnal or diurnal.

The arrangement of the anthers should ensure maximum pollen deposition on the pollinator and the stigma should be ideally positioned to receive it. This appears to be the situation for pohutukawa where the brush structure of the flowers and the inflorescence places a substantial amount of pollen over the chin and throat of the gecko and this part of the gecko's body is brushed across the stigmas as it searches for further nectar. For ngaio and flax the relationships of the anthers and stigmas seem less well adapted for pollen transfer by geckos, but from the amounts of pollen carried, especially of flax, it is probable that some pollination must occur.

Furthermore, flowers, or inflorescences, must be robust enough to support the weight of the pollinating gecko while feeding. This is certainly true of pohutukawa and flax which can easily support *Hoplodactylus duvauceli* (average weight of adults = 81 g (Whitaker 1968)) and *H. pacificus* (average weight of adults = 13 g (Whitaker 1968)).

None of the New Zealand plants from which geckos take nectar appear to be peculiarly adapted to pollination by lizards alone. On flax, geckos are perhaps best considered as very successful nectar "robbers" from a plant adapted to pollination by nectarivorous birds (bellbird (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*)) (McCann 1952; Godley 1979). The structure of ngaio flowers suggests insects are probably the primary pollinators — a number of insect species have been recorded visiting ngaio flowers (Heine 1937) — and on ngaio, geckos are again "robbers". The brush flowers of pohutukawa (and other *Metrosideros* spp.) are visited by nectarivorous birds and some insects (e.g., Thompson 1927; Heine 1937; McCann 1952; Gravatt 1970; Dugdale 1975; Godley 1979) but they do not seem to be specifically adapted for pollination by either group. Geckos appear to have the potential for effectively pollinating the brush-structured flowers of pohutukawa but, even if pollination is shown to occur, they would have to be regarded as "generalist" pollinators unless a close mutualism could be demonstrated. To determine whether there is a close relationship between brush-

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structured blossoms (either flowers or inflorescences) and lizard pollination, it would be valuable to reassess the primary pollinators of other brush-structured blossoms such as *Xeronema callistemon,* rewarewa (*Knightia excelsa:* Proteaceae) or kamahi (*Weinmannia racemosa:* Cunoniaceae).

Seed dispersal by lizards

To be effective as a seed disperser, an animal must transport (either internally or externally) seed beyond the parent plant, deposit it while still viable, and deposit it in a site where its chances of survival are good. A number of species of New Zealand lizards have been found to consume a variety of fleshy fruits. Neither the skinks nor the geckos that occur in New Zealand chew their food to any great extent and when small fruits are eaten they are invariably swallowed whole. Seeds from the fruits eaten by lizards are therefore not physically damaged when fruit is ingested, and pass through the gut intact. In many areas where lizards are common their droppings can be found crammed with seeds (Thomas 1982; Towns et al. 1984; pers. obs.) (Fig. 3). Tests with captive *H. maculatus* showed food passage times between 36–72 hours, although they are likely to be more rapid in summer when temperatures are higher and the lizards are more active (B. Goetz pers. comm.).

Studies elsewhere have shown that seeds which have passed through reptile guts are viable (Hnatiuk 1978; Clifford & Hamley 1982; Iverson 1985) or sometimes show enhanced viability (Rick & Bowman 1961; Rust & Roth 1981). The viability of seeds collected from the droppings of New Zealand lizards has not yet been thoroughly tested in germination trials by comparing them with the germination rates of seed collected directly from the plant. Nevertheless, sectioned seed from lizard droppings appears to be in excellent condition, and seeds of *Gaultheria ?antipoda, Muehlenbeckia axillaris, Leucopogon fraseri, Coprosma propinqua* and *Coriaria ?sarmentosa* from lizard droppings have been germinated in the laboratory: 48% (n = 25) of *Muehlenbeckia axillaris* seed from skink droppings germinated within 8 weeks, yet this is a species which is generally very difficult to germinate (M. Simpson pers. comm.). For *Gaultheria ?antipoda,* which normally germinates readily, two different samples each of 50 seeds showed 62% and 16% germination within 12 weeks (M. Simpson pers. comm.).

Although not as mobile as birds (the presumed dispersal vector of the seed of most fleshy fruits in New Zealand), lizards clearly have the ability to move well beyond the boundaries of the parent plant. For many species of geckos and skinks, sustained foraging movements of several metres over a few minutes are commonplace and during one foraging period a lizard may cover a substantial part of its home range (pers. obs.). *Leiolopisma grande* and *L. otagense* may make foraging movements of up to 15 m and 8 m, respectively (Towns et al. 1984). The longest recorded movement of a New Zealand lizard over a short time interval was of 73 m in 72 hours by *H. duvauceli* (Whitaker 1968). While birds can disperse seed long distances, between vegetation types or between remote patches of the same vegetation type, lizards are likely to be significant dispersal vectors only over short distances, within the one vegetation type or across an ecotone.

Lizard droppings containing seeds are often found many metres from the nearest source plant (e.g., Whitaker 1985), and are frequently deposited in sites which offer good prospects for seedling establishment. In one rock outcrop the crevices were littered with fresh droppings from *Hoplodactylus maculatus* containing numerous seeds of *Hymenanthera alpina* and *Coprosma propinqua* which were over 12 m uphill from the nearest fruiting plants (Fig. 3). Lizards have no aversion to defaecating in or near their retreats and large numbers of droppings containing seeds are found in sites such as cracks or crevices in rocks, deep within screes, beneath loose bark, and under logs and stones. In many environments, especially arid or exposed ones, these places provide the best conditions for germination and establishment of new plants. In rock crevices regularly inhabited by lizards, the debris from droppings accumulated over many years may provide an exceptionally fertile microsite for seedling establishment.

The only fruits known to be consumed by New Zealand lizards are those with sweet flesh, and this is clearly the reward for dispersing the seed. It is not immediately clear what attracts the lizards to the fruits as most are small (<5 mm diameter), more or less odourless, and generally white or translucent (some are pale blue or pale pink; *Leucopogon* is orange, *Coriaria* is nearly black).

Many of the species from which lizards take fruit are divaricating shrubs (e.g., *Coprosma* spp.) or tangled vines (e.g., *Muehlenbeckia* spp.). These plants may be adapted to seed dispersal by lizards because most of their fruits are borne on the inside of a dense tangle of branches and twigs in situations where it is impossible for frugivorous birds to get them. Indeed, Flux (1985) could think of no bird capable of taking the fruit of divaricating shrubs and wondered if geckos might do so. An extreme example is shown by *Hymenanthera alpina* which forms a compact and tightly-growing, low shrub bearing white fleshy berries on the underside of the stems close to the ground where they are well

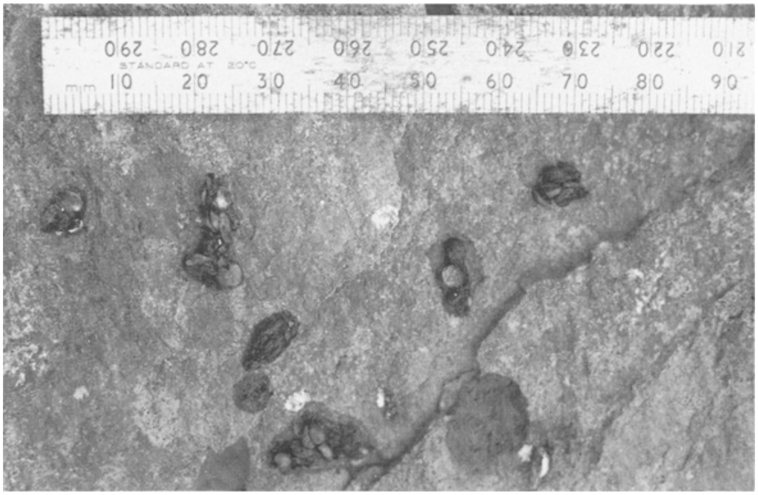

Fig. 3 Droppings of *Hoplodactylus maculatus* containing seeds of *Coprosma propinqua* (Rubiaceae) and *Hymenanthera alpina* (Violaceae) in a rock crevice.

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protected from birds by the dense tangle of strong, sharp twigs (Fig. 4). Additionally, *H. alpina* fruits close to the surface of the plant are frequently dark coloured on their upper surfaces making them more difficult to see from above. On the Canary Islands the fruit borne on pendulous branches close to the ground by *Plocama pendula* (Rubiaceae) was considered an adaptation to seed dispersal by lizards (Barquin & Wildpret 1975).

The present diversity and density of lizards over most of New Zealand is so low that it is hard to imagine they could be significant pollinators or seed dispersers. However, this has not always been the situation. Drastic habitat changes since the arrival of man in New Zealand, and the severe effects of introduced predators over the last 1000 years have brought about the extinction of at least one species (Bauer & Russell 1986), perhaps more (Worthy, in press); eliminated others from vast areas of their previous ranges (Whitaker 1978; Worthy, in press); and dramatically reduced the densities of most remaining species (Whitaker 1973; 1978). Lizard densities approximating those which must have occurred over much of New Zealand in primaeval times are now found at a very few mainland sites where there is good protective cover (e.g., Turakirae Head) and on relatively unmodified islands (e.g., Poor Knight's Islands). Only in such places is it possible to get an accurate idea of the role that lizards might have played in pollination and seed dispersal.

The density of geckos on flowering pohutukawa can exceed 5 m^{-2} of flowers. At this density the pollination capability over short distances may well exceed that of birds. At Turakirae Head the number of geckos in the highest density areas (boulder bank sites which are also the places where divaricating *Coprosma* spp. and *Muehlenbeckia* occur) have been calculated at 0.4 m^{-2} (Whitaker 1982) – 1.2 m^{-2} (Marshall 1983) and also occur sympatrically with two species of frugivorous skinks. At about one lizard m^{-2} nearly a million seeds ha^{-1} $year^{-1}$ will pass through lizard guts.

At Mt Kaukau, near Wellington, the large quantity of fruit drying on the divaricating shrubs was assumed to indicate the current dispersal agents were inefficient (Flux 1985). If these plants are truly adapted to seed dispersal by lizards then the overall reduction in the diversity and density of the lizard fauna could mean an inability of the lizards now present to cope with the fruit crop rather than any inefficiency in the dispersal of seeds they ingest.

The significance to the evolution of angiosperms of lizards acting as pollinators and seed dispersers has already been raised (Elvers 1977; Clifford & Hamley 1982, respectively). Sussman & Raven (1978) presumed that angiosperms with large flowers producing copious nectar evolved after the appearance of nectarivorous birds and mammals, and believed that bird and bat pollination had an early origin in the Myrtaceae. The observation of large numbers of geckos vigorously foraging on pohutukawa (Myrtaceae) nectar indicates that an early relationship between nectariferous angiosperm flowers and reptiles, as proposed by Hughes (1976), should be treated more seriously. The evolution of fleshy fruits in the Podocarpaceae and early New Zealand angiosperm genera (e.g., *Pseudowintera, Myrsine*) has so far only been considered in relation to bird dispersal (Clout 1982; Norton 1982). However, reptiles may also have

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Fig. 4 Branch of *Hymenanthera alpina* (Violaceae) turned over to show the white berries hanging beneath the stems. From above, these berries are protected from birds by a dense tangle of strong, sharp twigs.

been significant dispersers before the origin of birds, particularly in the Podocarpaceae (W. M. McEwen pers. comm.).

To conclude with a bit of speculation would be fun. *Fuchsia procumbens* is a rare, sprawling shrub for which the primary pollinator is unknown. *Fuchsia* spp. produce copious nectar and most members of the genus are believed to be bird pollinated (Raven 1979). However, no birds have been seen visiting the flowers of *Fuchsia procumbens* nor would they find it easy to do so as the flowers are borne at, or near, ground level and often within tangled branches. Furthermore, *F. procumbens* produces a fleshy berry which would be equally inaccessible to birds. Perhaps this is a species adapted to lizard pollination and seed dispersal?

Gunnera monoica is a small, perennial herb for which the seed dispersal vector is unknown. Most *Gunnera* spp. produce fleshy fruits which are brightly coloured, borne above the leaves, and are distributed by birds (C. J. Webb pers. comm.). In *G. monoica* the fruits are white and borne beneath the leaves where they are inaccessible to birds. Perhaps this is a species adapted to lizard dispersal?

The record of *Hoplodactylus duvauceli* eating a karaka fruit was isolated and probably exceptional, and certainly the animal could not have swallowed the seed let alone voided it elsewhere to germinate. However, a recently described, gigantic (and presumed extinct) gecko is believed to be from New Zealand and was probably arboreal (Bauer & Russell 1986). Other closely related, very large geckos in New Caledonia are known to be frugivorous (Bartmann & Minuth 1979; Bauer 1985) and this species may have been also. If so, it makes more plausible the Maori tales of large pet lizards that were fed on drupes such as tawa (*Beilschiemedia tawa:* Lauraceae) (White 1887). Perhaps in the primaeval forests of New Zealand giant geckos rivalled pigeons (*Hemiphaga novaeseelandiae*), and other birds as the dispersers of the very large fleshy fruits?

The observations documented here are based almost entirely on research into the ecology and diet of New Zealand lizards and not on studies of the reproductive biology of the plant species involved. They do not demonstrate that pollination or seed dispersal by lizards actually occurs but clearly indicate the possibilities which exist. Hopefully this paper will create an awareness amongst botanists of the potential roles of lizards in the reproductive strategies of some New Zealand plants which will stimulate further research.

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NOTE ADDED IN PRESS:

Recent observations show pollen should not be entirely discounted as a food source for New Zealand geckos. Gardner (1984) has found that for at least four species of *Phelsuma* (*sundbergi, astriata, laticauda* and *abbotti*) pollen from several species of palm is a major component of the diet under suitable conditions. *Phelsuma* geckos actively seek out palm inflorescences and vigorously defend them from other lizards. On Stephens Island, Cook Strait, in February 1987, M. B. Thompson (pers. comm.) observed *Hoplodactylus maculatus* congregating nightly on the flowers of nikau (*Rhopalostylis sapida* : Palmae), with as many as eight geckos on each inflorescence. It is not known whether they were feeding on nectar or pollen but smears from the throats of three animals showed some nikau pollen was being carried.

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