

Effectiveness of the common gecko (*Hoplodactylus maculatus*) as a seed disperser on Mana Island, New Zealand

DEBRA M. WOTTON

School of Biological Sciences
Victoria University of Wellington
P.O. Box 600
Wellington, New Zealand

Present address: 28 Fairburn Grove, Johnsonville,
Wellington 6004, New Zealand.

Email: debrawotton@yahoo.co.nz

Abstract A number of recent studies have documented frugivory by lizards and the effect on seed viability. However, few studies of seed dispersal by lizards have investigated the quantitative and qualitative components of disperser effectiveness. I investigated the role of *Hoplodactylus maculatus* (common gecko) in frugivory and seed dispersal by measuring levels of fruit removal, dispersal distances, and the effects of gut passage and seed deposition patterns on germination success. Common geckos appeared to be the major frugivore of *Coprosma propinqua*, removing large quantities of fruit. Forty percent of gecko droppings collected contained seeds, over 95% of which were from *C. propinqua*. Common geckos dispersed *C. propinqua* seeds up to at least 9.3 m. Ingestion of *C. propinqua* seeds by common geckos had no effect on germination success, with 72% of seeds germinating. Geckos tend to deposit seeds beneath rocks; these microhabitats appear to be suitable for germination of *C. propinqua*, with high levels of mean seed germination (73%). These results provide strong evidence that fruit is an important component of the diet of *Hoplodactylus maculatus*, and that common geckos provide effective seed dispersal for *C. propinqua*.

Keywords seed dispersal; lizards; frugivory; *Hoplodactylus maculatus*; common gecko; disperser effectiveness; *Coprosma propinqua*

INTRODUCTION

Disperser effectiveness, the contribution a disperser makes to a plant's future reproduction, has both quantitative and qualitative components (Schupp 1993). Seed dispersal quantity depends on the number of visits a disperser makes, and the number of seeds dispersed per visit. Dispersal quality depends on the treatment of seeds in the disperser's mouth and gut, and seed deposition patterns (Schupp 1993).

Although there are many reports on the effect of gut passage on seed viability (Iverson 1985; Whitaker 1987; Traveset 1990, 1995; Figueira et al. 1994; Valido & Nogales 1994; Willson et al. 1996; Nogales et al. 1998; Castilla 1999), few studies of seed dispersal by lizards have investigated the quantitative and qualitative components of seed dispersal that define disperser effectiveness (see Figueira et al. 1994 for investigation of some components).

The opportunity exists for seed dispersal by lizards to occur in New Zealand, due to a local radiation of lizard taxa (Hickson & Slack 1998) and relatively depauperate avian (Clout & Hay 1989) and mammalian seed disperser faunas. Lizards in New Zealand consume large amounts of fruit on a seasonal basis, although it has not been demonstrated that they are capable of effective seed dispersal (Whitaker 1987).

Divaricating plants consist of a dense tangle of interlacing twigs, branching at a wide angle. The divaricate growth form is unusually common in New Zealand, with divaricating species belonging to 20 genera in 17 families and comprising 10% of the flora (Greenwood & Atkinson 1977). Whitaker (1987) suggested that some divaricating plants that possess fleshy fruits characteristic of vertebrate dispersal might be adapted to seed dispersal by lizards. The fruit of divaricating shrubs is often inconspicuous, due to its location on the underside of branches and deep within the plant. When combined with the tightly interwoven branching pattern, this appears to inhibit access to fruit of divaricating plants by frugivores other than lizards.

Flux (1985) could think of no bird capable of taking the fruit of divaricating plants.

Howe & Smallwood (1982) hypothesised three advantages of seed dispersal: (1) the "escape hypothesis" predicts that the selective advantage of dispersal is avoiding disproportionate seed and seedling mortality near the parent, due to competition with parents or siblings; (2) colonising disturbed sites; and (3) locating fixed microhabitats suitable for establishment and growth. Directed dispersal (3) may be important if specific conditions are required for seed germination or survival. Lizard droppings containing seeds are frequently deposited in sites that appear to provide good conditions for germination and establishment, especially in arid or exposed environments (Whitaker 1987).

The principal goal of this study was to investigate the effectiveness of *Hoplodactylus maculatus* (Gray, 1845), the common gecko, in seed dispersal of some fleshy-fruited native plant species. I approached this aim by testing two sets of hypotheses.

Set one: Frugivory: composition and quantity

- 1 Common geckos consume fruit of both *Coprosma propinqua* Cunn. (Rubiaceae) and *Muehlenbeckia complexa* (Cunn.) Meissner (Polygonaceae).
- 2 Fruit is an important component of the diet of common geckos.
- 3 Lizards are capable of removing most available *C. propinqua* fruit in the absence of birds.

Set two: Dispersal effectiveness

- 1 Common geckos disperse large numbers of seeds.
- 2 Common geckos disperse seeds away from the parent plant.
- 3 Common geckos deposit seeds in sites that enhance germination success.
- 4 Seeds pass through common geckos intact, and with enhanced germinability.

METHODS

Study site

This study was conducted on Mana Island (41°6'S, 174°48'E) from February to August 1999. Mana Island is a 217-ha scientific reserve situated about 2.5 km offshore, north of Wellington, New Zealand. Mana Island was intensively farmed from 1832 to 1986 (Timmins et al. 1987), creating a highly modified environment that is currently undergoing ecological restoration. A plague of mice was eradicated from

Mana Island in 1989–1990, leaving the island mammal free (Newman 1994). The study site was located on a shore platform on the eastern side of Mana Island. This exposed, coastal habitat consists of rank exotic grasses and regenerating *C. propinqua* and *M. complexa*, interspersed with stony patches.

Study plants

Coprosma propinqua is a divaricating, dioecious shrub, up to 7 m tall, found throughout New Zealand (Poole & Adams 1990) in open communities, shrubland, and forest margins (Greenwood & Atkinson 1977). Many plants at the study site were prostrate, a common growth form in coastal areas. Female plants produced ripe fruit from February to April (DMW pers. obs.). The fruit consists of drupes that range in colour, both within and among plants, from white to pale blue or white with blue flecks, to deep purple and nearly black. Each fruit usually contains two, or occasionally three, seeds. Drupes are globose (Allan 1961) and about 3–7 mm maximum diam. (Allan 1961; DMW unpubl. data).

Muehlenbeckia complexa is a climber forming compact masses, found throughout New Zealand. The flowers consist of a white five-partite perianth, becoming succulent beneath the fruit, which consists of a black three-angled nut (Poole & Adams 1990). The fruit is about 2 mm at the longest axis (Allan 1961), excluding the fleshy portion.

Study animal

Hoplodactylus maculatus (common gecko) is a small (up to c. 75 mm snout-vent length on Mana Island (DMW unpubl. data)), nocturnal gecko. This species was previously thought to be widespread throughout New Zealand (Whitaker 1982); it has now been established that a complex of more localised species exists (Hitchmough 1997). The Mana Island population belongs to the species that retains the name *Hoplodactylus maculatus* (Hitchmough 1997).

The common gecko is primarily terrestrial although it is quite at home in trees in forested habitats (Whitaker 1982). Its diet is omnivorous, with fleshy fruits, including those of *Coprosma* and *Muehlenbeckia*, of seasonal importance (Whitaker 1982). The common gecko is widespread and extremely abundant on Mana Island (Newman 1994).

Frugivory

A frugivore exclusion experiment was set up on Mana Island to quantify the consumption of *C. propinqua* fruit by common geckos. The exclusion

experiment involved a blocked design with three treatments per plant (with individual plants as blocks): a branch from which all frugivores were excluded with fine mesh bags (A), a branch from which birds were excluded with chicken-wire cages (B), and an unexclosed branch (C). This design was replicated on 15 plants.

In addition to excluding frugivores, Treatment A allowed the measurement of natural fruit fall over the period of the experiment by retaining abscised fruit. Treatment B measured fruit removal by geckos and skinks (which also occur in the study site) and naturally abscised fruit. Lizards are the only potential frugivores other than birds on Mana Island, as the island is rodent-free. Wire cages with hexagonal apertures of c. 2.5×3.5 cm at the widest points were secured around branches, enclosing a volume of approximately 2 litres. A buffer zone of at least 10 cm was established between the cage and each experimental branch, to prevent birds from reaching through the apertures to eat fruit.

The number of fruit on all experimental branches was counted at the start of the experiment and again after 10 weeks. At the end of the experiment all remaining fruit were categorised as unripe (fruit still green), ripe, or shrivelled. Any unripe fruit at the end of the experiment were counted as being unavailable for consumption and were removed from the data set before analysis.

Dispersal quantity

The quantity of seeds dispersed by the common gecko was obtained using data from droppings collected during pitfall trapping (see below). Densities of seeds dispersed by common geckos were calculated by determining the number of seeds collected per unit trap area.

Dispersal quality

Pitfall traps consisting of 4-litre plastic paint containers (22 cm diam.), each partially covered with a large rock, were set around fruiting shrubs at the study site. Five plants each of *C. propinqua* and *M. complexa* were selected; traps were placed 0 m, 0.5 m, and 1 m from the edge of each plant's crown and each trap on a different, random compass bearing. In addition, distances were also measured from each trap to the nearest non-target species, allowing dispersal distances of up to 19.5 m to be measured. Plants at the study site were generally closely spaced, impeding placement of traps at distances greater than 1 m from the nearest fruiting plant.

Traps were set in the early evening, baited with tinned pear and cat food, and checked the following morning. Between trapping sessions a stick was placed in each trap to allow animals to become familiar with traps whilst being able to escape. Pitfall trapping was carried out for a total of 17 nights from mid February to late April. Gecko droppings were collected from set traps and from trapped geckos, which were held for up to 48 hours, and any seeds counted and identified. There is no difference in appearance to distinguish *H. maculatus* droppings and those of skinks. However, as skinks are unable to climb out of traps (although geckos often do), droppings in traps were collected only when no skinks were present.

The effect of gecko consumption on *C. propinqua* seed viability was tested by sowing 134 *C. propinqua* seeds in each of three treatments: seeds collected from gecko droppings, seeds from *C. propinqua* plants with the flesh removed (to simulate the physical action of gecko consumption on seeds), and intact fruit collected from plants. Seeds were sown in a glasshouse in late March 1999 in separate trays containing potting mix. The trays were moved to a different glasshouse in early June 1999, as the original glasshouse was heated and appeared to be inhibiting germination. Once moved, the numbers of germinated seeds in each treatment were recorded twice a week.

A seed germination experiment was set up on Mana Island to determine whether *C. propinqua* seed deposition in different microhabitats has any effect on germination. The experiment involved a randomised block design with four microsite treatments per spatially separated block (site): wedged down between rocks (rock), amongst rank exotic grass (grass), underneath fruiting *C. propinqua* plants (Coppro), and under *M. complexa* plants (Muecom). The experiment was replicated in 15 sites, with an additional 5 control sites (see below). This experiment did not specifically test the effects of substrate on seed germination, but rather tested the effects of microclimatic conditions in each microhabitat.

Due to the patchy distribution of microhabitats within the study area, I selected 28 sites where the four microsite types occurred in close proximity. Of these 28 sites, 20 were randomly selected for the study, 15 to receive seeds and 5 as controls. Ten *C. propinqua* seeds were placed in each of four pots at each of the 15 treatment sites. The four pots at each of the five control sites lacked seeds to control for any seeds entering from the seed rain. An additional

set of 20 pots (15 with seeds and 5 without) was placed in a glasshouse to compare germination under field conditions with the potential germination of *C. propinqua* seeds.

Each pot was half filled with soil from the study area, with an additional layer of approximately 2 cm of soil on top. The top layer of soil (also from the study area) was sterilised by oven baking at 180°C for one hour, then watered, left overnight, and baked for a further hour, to eliminate the possibility of seeds germinating from the seed bank. The five pots in the glasshouse that lacked *C. propinqua* seeds checked the success of the soil sterilisation process.

Table 1 Mean (\pm SE) percent ripe fruit loss for the three treatments used in the frugivore exclusion experiment: A (all frugivores excluded), B (birds excluded), and C (open access) ($N = 15$).

Treatment	% ripe fruit loss
A	46.62 \pm 5.09
B	93.27 \pm 2.40
C	96.02 \pm 5.96

Statistical analysis

Data from the exclusion experiment were analysed using SAS statistical packages (SAS Institute 1995). Germination experiment and microsite experiment data were analysed using SigmaStat (SPSS Inc. 1997).

Exclusion experiment data were arcsine transformed after testing for normality. Data were then analysed using a two-tailed ANOVA, with plant as a blocking variable, to explain the percentage of ripe fruit removed in terms of treatment.

Germination success for the three treatments in the germination experiment was compared using a

Table 2 Results of an ANOVA for effects of experimental treatments A (control branches with complete frugivore exclusion), B (branches from which birds were excluded), and C (unexcluded branches) on ripe fruit loss using arcsine transformed data ($N = 15$).

Source	d.f.	<i>F</i>	<i>P</i>
Plant	14	0.96	0.5133
Treatment	2	60.23	0.0001
Contrast A versus B+C	1	119.70	0.0001
Contrast B versus C	1	0.76	0.3908

Table 3 Gecko droppings containing seeds of 3 plants, showing mean (\pm SE) number of seeds per dropping, and mean (\pm SE) dispersal distances of individual seeds and droppings containing seeds. An unequal number of traps were placed at greater distances from each species.

Source	Mean value \pm SE	Range	<i>n</i>
<i>Coprosma propinqua</i>			
No. seeds per dropping	2.61 \pm 0.24	1–9	56
Dispersal distance (m)			
seeds	1.82 \pm 0.21	0–9.3	144
droppings	1.95 \pm 0.37	0–9.3	55
<i>Muehlenbeckia complexa</i>			
No. seeds per dropping	1.00 \pm 0	1	3
Dispersal distance (m)			
seeds	1.05 \pm 0.28	0.5–1.35	3
droppings	1.05 \pm 0.28	0.5–1.35	3
<i>Phytolacca octandra</i>			
No. seeds per dropping	1.33 \pm 0.33	1–2	3
Dispersal distance (m)			
seeds	14.11 \pm 3.52	3.75–19.5	4
droppings	13.28 \pm 4.84	3.75–19.5	3
Total			
No. seeds per dropping	2.63 \pm 0.26	1–10	60
Dispersal distance (m)			
seeds	1.98 \pm 0.27	0–19.5	151
droppings	2.54 \pm 0.51	0–19.5	59

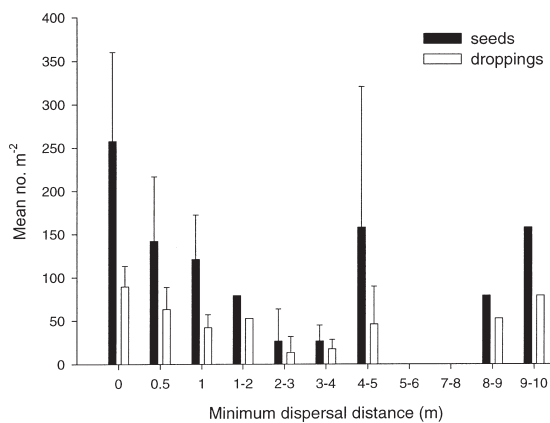


Fig. 1 Mean density of *Coprosma propinqua* seeds and droppings containing seeds dispersed by *Hoplodactylus maculatus* at set dispersal intervals. Error bars are 1 SEM.

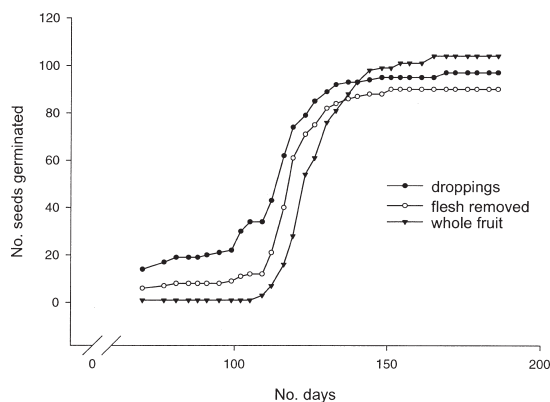


Fig. 2 Germination rates of 134 *Coprosma propinqua* seeds sown in each of three treatments: collected from gecko droppings; collected directly from plants with the flesh removed; and whole fruit collected from plants. Seed germination was recorded twice a week over the period of the experiment.

chi-square test. After testing for normality, data from the microsite experiment were arcsine transformed, then analysed using a two-way ANOVA with site as a blocking variable. Differences between treatments were then compared using a Tukey Test. The microsite with the highest mean germination was compared with potential germination (in the glasshouse) using a *t*-test.

RESULTS

Frugivory

In the absence of frugivores, 47% of ripe fruit fell naturally (Table 1). However, the rate of fruit loss in the total exclusion treatment (A) was significantly less than in both the bird exclusion treatment (B) and the open access treatment (C) (Table 2). There was no significant difference between fruit loss from branches where birds were excluded, and branches accessible to all frugivores. The effect of plant on variation in fruit loss was negligible.

Dispersal quantity

A total of 98 geckos were trapped during 510 trap-nights, over a period of 10 weeks. One hundred and fifty-four gecko droppings were collected through pitfall trapping, of which 60 (38.96%) contained seeds. Sixty-one (39.61%) droppings contained fruit

remains (including seeds). Twenty of the droppings containing seeds were collected from trapped geckos held overnight, with the remainder collected from traps. All seeds collected from gecko droppings were intact, and looked like uningested seeds. Over 95% of the seeds found in gecko droppings were from *C. propinqua*, with remaining seeds from *M. complexa* and *Phytolacca octandra* (Phytolaccaceae, inkweed). Few *M. complexa* plants at the study site had ripe fruit during the trapping period.

The mean number of seeds per dropping was 2.63 (Table 3), with a mean of 2.61 *C. propinqua* seeds per dropping. The mean density of *C. propinqua* seeds dispersed by geckos was 98 seeds m⁻² over the 17 nights that traps were set. The highest densities of dispersed *C. propinqua* seeds and gecko droppings containing seeds were 258 seeds and 89 droppings m⁻², respectively (Fig. 1). Although the greatest seed densities were found nearest to fruiting shrubs, high seed densities were also found further from *C. propinqua* plants.

Dispersal quality

Common geckos dispersed *C. propinqua* seeds 0 to 9.3 m (minimum dispersal distance) from the edge of the plant's crown. The mean dispersal distance of *C. propinqua* seeds and droppings containing *C. propinqua* seeds was 1.65 m and 1.95 m, respectively (Table 3).

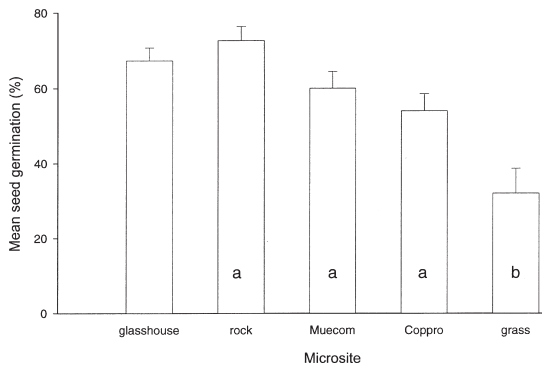


Fig. 3 The effect of microhabitat on germination success of *Coprosma propinqua* seeds. Different letters indicate significant differences between microhabitats in the field ($P < 0.001$). Differences in germination success between seeds in the glasshouse and in the “rock” microsite were compared using a t -test (no significant difference; $P = 0.301$). Error bars are 1 SEM. Muecom, under *Muehlenbeckia complexa*; Coppro, under *Coprosma propinqua*.

Germination success was not affected by seed treatment ($\chi^2 = 3.144$, $P = 0.208$). There was no significant difference in the number of seeds that germinated from gecko droppings (97, 72%) compared with those collected from plants, both with the flesh removed (90, 67%), and from whole fruit (103, 77%). However, treatment affected the rate of seed germination (Fig. 2). Seeds from droppings germinated faster than seeds collected from the plant, both with the flesh removed and from intact fruit. Seeds from plants with the flesh removed germinated faster than those from intact fruit.

In the microsite germination experiment, mean germination of seeds in the grass treatment was significantly lower than that in the other three treatments ($F = 11.292$, $P < 0.001$) (Fig. 3). No significant differences were detected between the other microsites. Site (= block) had no significant effect on the variation in germination success ($F = 0.927$, $P = 0.539$).

The highest mean field germination (in the “rock” microsite) did not differ significantly from germination in “ideal” conditions in the glasshouse ($t = -1.053$, $P = 0.301$). Two of the control pots placed in the field each contained a germinated *C. propinqua* seed. Both pots were underneath a *C. propinqua* plant. No seeds germinated from control pots in the glasshouse.

DISCUSSION

Lizards have seldom been considered as frugivorous, and even less as having the potential to act as legitimate seed dispersers. This study strongly suggests that common geckos play an important role in frugivory and local or short-distance seed dispersal of *C. propinqua*.

Frugivory

A study of gut contents of common geckos at Turakirae in Wellington (Whitaker 1987) found that of those geckos that contained food up to 65% had eaten fruit. As hypothesised, fruit was an important component in the diet of the common gecko population on Mana Island during the study period (approximately 40% of droppings contained seeds), indicating that fruit consumption by *H. maculatus* is widespread. Fruit of both *Coprosma* and *Muehlenbeckia* was seasonally important in the diet of common geckos at Turakirae (Whitaker 1982). Geckos on Mana Island consumed large amounts of *C. propinqua* fruit. However, few seeds of *M. complexa* were found in droppings, as most of the fruit was not ripe during pitfall trapping.

The frugivore exclusion experiment supported the hypothesis that lizards are capable of removing most available *C. propinqua* fruit. Exclusion of birds had no effect on *C. propinqua* fruit removal rates, and birds were seldom observed in the study site during the 1999 fruiting season. It appears that birds consume few *C. propinqua* fruit in coastal shrubland habitat, although the fruit is consumed in other habitat types (Ferguson & Drake 1999). Birds are likely to be able to remove the small proportion of fruits that occur on the exterior of each plant.

With natural fruit fall of 47%, a conservative estimate of fruit removal by lizards is obtained by subtracting this amount from observed levels of fruit loss in the absence of birds. Lizards therefore removed at least 46% of *C. propinqua* fruit. However, actual levels of fruit removal may be considerably higher, especially as fruit that dehisces naturally is readily consumed by lizards (Whitaker 1987) and may be unavailable to other vertebrate dispersers if it falls beneath the plant’s canopy.

It was not possible to determine exactly how much of this frugivory was attributable to common geckos, as skinks also occurred in the study site. However, skinks are likely to be much less important as frugivores than geckos, partly due to their poorer climbing ability (Whitaker 1987). Lawrence (1997) found that geckos consumed more fruit than skinks

in feeding trials. Geckos in this study consumed more fruit than did skinks on nearby Matiu-Somes Island (D. R. Drake and O. Thomson unpubl. data) (39% and 12% of droppings with seeds, respectively). This was not due to a lack of fleshy-fruited plants on Matiu-Somes.

Dispersal quantity

Dispersal quantity depends on the number of visits a disperser makes and its fruit removal rate (Schupp 1993). The number of visits is a function of the abundance and reliability of the disperser (Schupp 1993). Although common geckos appear to remove relatively small quantities of fruit at a time (droppings contained a mean of c. 2.5 seeds, which equates to just over 1 fruit of *C. propinqua* per dropping), they are extremely abundant on Mana Island. Gut passage rates of fruit through common geckos are inversely correlated with temperature, and can range up to several days (Lawrence 1997). The high level of fruit removal in the absence of birds suggests that common geckos are reliable visitors to *C. propinqua*.

Ferguson (1998) found that starlings deposited *C. propinqua* seeds (total deposition during January and February 1998) at a mean density of 366 seeds m^{-2} on Mana Island. The starling population on Mana has been estimated to number tens of thousands of birds. After adjusting figures to account for continuous versus intermittent sampling, the density of common gecko seed deposition (392 seeds m^{-2}) is equivalent to the level of seed deposition by starlings. However, seed densities measured in this study may not be reliable indicators of actual densities of seed deposition by common geckos. Seed densities by geckos were artificially high for two reasons: all individuals were removed from traps and held for up to 48 hours, some for a shorter period. Not all seeds may have been defecated in the allocated trap (and therefore at the measured distance) during this time. In addition, traps acted as seed “sinks”; if trapped geckos were free to move then seeds may have been spread over a wider area. A third of all droppings containing seeds were collected from individuals held for up to 48 hours. The remainder were collected from traps where geckos had entered and were still there or had subsequently climbed out.

Dispersal quality

Seed dispersal quality depends on the effect of passage through the mouth and gut of the disperser, and patterns of seed deposition (Schupp 1993). Results from the germination experiment did not

support the hypothesis that passage of seeds through the gut of common geckos enhances germination. However, ingestion of *C. propinqua* seeds by *Hoplodactylus maculatus* had no detrimental effect on germination success, with seeds passed intact and high proportions of seeds germinating in all treatments. Numerous studies of seed dispersal by lizards have tested the effect of gut passage on seed viability. Consumption by lizards increased seed viability in some plant species (Figueira et al. 1994; Valido & Nogales 1994) and decreased viability in others (Valido & Nogales 1994), with seeds of most plant species remaining unaffected (Iverson 1985; Valido & Nogales 1994; Willson et al. 1996; Nogales et al. 1998; Castilla 1999; this study).

Seed passage through geckos increased the germination rate compared with seeds collected directly from the plant. However, a difference of three days in the germination rate is unlikely to have any effect on seed survival or growth as *C. propinqua* seeds take months to germinate. Consumption of *Lycium intricatum* fruit by the lizard *Gallotia atlantica* decreased the rate of germination compared with seeds collected directly from plants (Nogales et al. 1998). This was more likely to affect germination success as most *L. intricatum* seeds germinated within three weeks.

Dispersal distance from the parent plant can have a significant effect on the germination and survival of seeds. Escape from the parent may be important if seeds are subject to density-dependent mortality (due to predation, pathogen attack, or competition with the parent or siblings), or “distance-responsive” predation (Howe & Smallwood 1982). Common geckos disperse *C. propinqua* seeds well beyond the crown of the parent plant, though most seeds appear to be deposited close to the source. At this time it is not known whether *C. propinqua* seeds benefit from increased dispersal distances from the parent. However, germination was not adversely affected beneath the parent plant, and many plants at the study site grow so closely together that it is difficult to distinguish individuals.

Dispersal distances obtained in this study were limited by two factors: the placement of pitfall traps, and the nearest seed source. Seeds were obtained in *Hoplodactylus maculatus* droppings at the maximum possible distance allowed by the placement of pitfall traps. Greater distances may have been measured with traps further from the nearest fruiting plant. All distances measured were minima as measurements were taken to the nearest fruiting plant, which was not necessarily the seed source. The few seeds of

Phytolacca octandra found in gecko droppings show that greater dispersal distances are possible. These plants were uncommon in the study site, and identification of the seed source was therefore more likely to be accurate. Whitaker (1982) reported occasional movements by the common gecko of over 20 m.

Long-distance seed dispersal by lizards is unlikely, as their movements are small relative to other seed dispersers such as birds. Droppings of the lizard *Tropidurus torquatus* containing seeds of *Melocactus violaceus* were found up to 6.9 m away from the nearest plant (Figueira et al. 1994). *Hoplodactylus maculatus* are capable of dispersal within a habitat, and across ecotones.

Patterns of seed deposition can affect the survival and germination of seeds. Seed deposition may vary in the number and species composition of seeds deposited, and the place of deposition (Schupp 1993). Gecko droppings contained fewer seeds than bird droppings and they were deposited in smaller clumps (DMW pers. obs.). Seed deposition by geckos may increase the success of individual seeds by reducing density-dependent mortality (Howe & Smallwood 1982).

Seed dispersal directed towards specific microhabitats can be advantageous for seed germination and survival (Howe & Smallwood 1982). Use of disparate habitats by frugivores can result in differential microhabitat seed deposition (Fialho 1990). Geckos retreat underneath rocks during the daytime. They are thigmothermic, and gain heat from pressing against the rocks. Droppings tend to be defecated in these retreats, leaving behind any seeds present.

Differential patterns of seed deposition can subsequently affect seed germination (Fialho 1990). Common geckos deposit seeds where microsite conditions enabled successful germination of *C. propinqua* seeds. Germination between rocks was higher even than for seeds germinated under supposedly ideal conditions in the glasshouse, although the difference was not significant. As much of Mana Island is covered in rank exotic grassland, under which germination of *C. propinqua* seeds is inhibited, natural regeneration is likely to be limited until grass cover is replaced by native plantings. Differences in germination success in this experiment were due to microclimatic effects, not substrate, as a standard soil medium was used. Although the effects of substrate were not tested, *C. propinqua* seeds germinate naturally from amongst

these rocks (pers. obs.). Adult *C. propinqua* plants present in these microsites provide evidence that some of these seedlings can survive to adulthood (pers. obs.).

Fialho (1990) found that seed deposition patterns exhibited by the lizard *Tropidurus torquatus* adversely affected seed germination in a coastal sand dune habitat compared with dispersal by a treefrog. *T. torquatus* tended to deposit seeds on sandy substrates in the open where few seeds germinated, while seed dispersal by the treefrog was directed toward the moist interior of bromeliads where germination was much higher.

Results from the present study support some of the hypotheses on the effectiveness of common geckos as seed dispersers. Although neither gut passage through nor seed deposition by *H. maculatus* significantly increased germination success, no detrimental effects were observed. Common geckos provided effective local seed dispersal for *C. propinqua* by moving large quantities of intact, viable seeds away from the parent plant and depositing them in sites where successful germination occurred.

ACKNOWLEDGMENTS

Don Drake, Kim McConkey, Rod Hitchmough, Tony Whitaker, and Corinne Watts provided helpful comments on earlier drafts. Thanks to Corinne Watts, Dean Benvenuti, and Nadia Jones for help with fieldwork. Department of Conservation Wellington Conservancy gave permission for the research to be conducted, and staff on Mana Island provided logistical support during fieldwork. Christa Mulder assisted with statistical analyses. Valuable advice on reptiles was gratefully received from Dave Towns, Rod Hitchmough, and Tony Whitaker. Barry Sneddon kindly identified inkweed plants. This research received financial assistance from School of Biological Sciences, Victoria University of Wellington, and Wellington Botanical Society.

REFERENCES

- Allan, H. H. 1961: Flora of New Zealand. Vol. I. Wellington, Government Printer.
- Castilla, A. M. 1999: *Podarcis lilfordi* from the Balearic islands as a potential disperser of the rare Mediterranean plant *Withania frutescens*. *Acta Oecologia* 20: 103–107.

- Clout, M. N.; Hay, J. R. 1989: The importance of birds as browsers, pollinators, and seed dispersers in New Zealand forests. *New Zealand Journal of Ecology* 12 (Supplement): 27–33.
- Ferguson, R. N. 1998: Influence of vegetation structure on spatial patterns of bird-dispersed seeds on Mana Island, New Zealand. Unpublished BSc(Hons) project, Victoria University of Wellington, Wellington, New Zealand.
- Ferguson, R. N.; Drake, D. R. 1999: Influence of vegetation structure on spatial patterns of seed deposition by birds. *New Zealand Journal of Botany* 37: 671–677.
- Fialho, R. F. 1990: Seed dispersal by a lizard and a treefrog — effect of dispersal site on seed survivorship. *Biotropica* 22: 423–424.
- Figueira, J. E. C.; Vasconcellos-Neto, J.; Garcia, M. A.; de Souza, A. L. T. 1994: Saurocory in *Melocactus violaceus* (Cactaceae). *Biotropica* 26: 292–301.
- Flux, I. A. 1985: Divaricating shrubs of Mt. Kaukau — observations and interpretations. Unpublished BSc(Hons) project, Victoria University of Wellington, Wellington, New Zealand.
- Greenwood, R. M.; Atkinson, I. A. E. 1977: Evolution of divaricating plants in New Zealand in relation to moa browsing. *Proceedings of the New Zealand Ecological Society* 24: 21–33.
- Hickson, R.; Slack, K. 1998: Phylogeny recapitulates geography — New Zealand's skinks in the Oligocene. In: Cooper, R. A.; Jones, C. M. ed. *Geology and genes: extended abstracts of papers presented at the Geogenes 98 Conference*, Science House, Wellington, Tuesday 24 March 1998. *Geological Society of New Zealand Miscellaneous Publication* 97.
- Hitchmough, R. A. 1997: A systematic revision of the New Zealand Gekkonidae. Unpublished PhD thesis, Victoria University of Wellington, Wellington, New Zealand.
- Howe, H. F.; Smallwood, J. 1982: Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.
- Iverson, J. B. 1985: Lizards as seed dispersers? *Journal of Herpetology* 19: 292–293.
- Lawrence, M. H. 1997: The importance of lizards to seed dispersal of native montane fleshy fruits, Canterbury, New Zealand. Unpublished MSc thesis, University of Canterbury, Christchurch, New Zealand.
- Newman, D. G. 1994: Effects of a mouse, *Mus musculus*, eradication programme and habitat change on lizard populations of Mana Island, New Zealand, with special reference to McGregor's skink, *Cyclodina macgregori*. *New Zealand Journal of Zoology* 21: 443–456.
- Nogales, M.; Delgado, J. D.; Medina, F. M. 1998: Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canary Islands). *Journal of Ecology* 86: 866–871.
- Poole, A. L.; Adams, N. M. 1990: Trees and shrubs of New Zealand. 2nd ed. Wellington, DSIR Publishing.
- SAS Institute 1995: SAS/STAT user's guide. Release 6.1 edition. Cary, North Carolina, USA, SAS Institute.
- Schupp, E. W. 1993: Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107: 15–29.
- SPSS Inc. 1997: SigmaStat 2.0 for Windows User's Manual. USA, SPSS Inc.
- Timmins, S. M.; Atkinson, I. A. E.; Ogle, C. C. 1987: Conservation opportunities on a highly modified island: Mana Island, Wellington, New Zealand. *New Zealand Journal of Ecology* 10: 57–65.
- Traveset, A. 1990: *Ctenosaura similis* Gray (Iguanidae) as a seed disperser in a Central American deciduous forest. *American Midland Naturalist* 123: 402–404.
- Traveset, A. 1995: Seed dispersal of *Cneorum tricoccon* L. (Cneoraceae) by lizards and mammals in the Balearic islands. *Acta Oecologia* 16: 171–178.
- Valido, A.; Nogales, M. 1994: Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos* 70: 403–411.
- Whitaker, A. H. 1982: Interim results from a study of *Hoplodactylus maculatus* (Boulenger) at Turakirae Head, Wellington. In: Newman, D. G. ed. *New Zealand herpetology — proceedings of a symposium held at the Victoria University of Wellington 29–31 January 1980*. *New Zealand Wildlife Service Occasional Publication* 2: 363–374.
- Whitaker, A. H. 1987: The role of lizards in New Zealand plant reproductive strategies. *New Zealand Journal of Botany* 25: 315–328.
- Willson, M. F.; Sabag, C.; Figueroa, J.; Armesto, J. J.; Caviedes, M. 1996: Seed dispersal by lizards in Chilean rainforest. *Revista Chilena de Historia Natural* 69: 339–342.