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SHORT COMMUNICATION

Seed retention times in New Zealand's largest gecko, *Hoplodactylus duvaucelii*, and implications for seed dispersal

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Abstract: Fruit is an important component in the diet of many lizards, but their role as seed dispersers is often overlooked. Seed retention time and animal movement determine how far a fleshy fruited seed will be dispersed from the parent plant. Seed retention times were investigated in 78 captive *Hoplodactylus duvaucelii* (Duvaucel's geckos). Geckos were offered fruits from 10 plant species. Fifty-one geckos consumed fruits and the mean seed retention time was 69 hours (range 31 to 145 hours). There was no difference between the mean seed retention in adult males and females, but juvenile geckos had significantly shorter mean seed retention times. There was no relationship between seed retention time and body mass in adult geckos. Based on their seed retention times, we suggest Duvaucel's geckos and other native lizards with body mass ≥ 14 g could disperse seeds over 10 m away from the parent plant.

Keywords: Duvaucel's gecko, gut passage time, lizard, reptile

Introduction

There is significant interest worldwide in how declines in birds and mammals affect plant species dispersed by frugivory. Fleshy fruits are also an important component in the diet of lizards and the role of lizards as seed dispersers is beginning to be recognised (Valido & Olesen 2007, 2019), including in New Zealand (Whitaker 1987; Wotton et al. 2016). However, there is little information on the plant species New Zealand lizards disperse or their effectiveness as seed dispersers. For its land area, New Zealand has the highest richness of reptile species globally (Towns & Daugherty 1994); thus, seed dispersal by reptiles may be more prevalent than elsewhere (Thorsen et al. 2011). Seed retention time (the period between ingestion and defecation) is one component of seed dispersal effectiveness, which is the contribution of the disperser to the plant's fitness, in terms of the number of new recruits produced (Schupp et al. 2017). Dispersal effectiveness includes quantity components (immediate outcomes of seed dispersal, e.g. the number of seeds eaten) and quality components (long-term post-interaction outcomes that determine the number of new recruits, e.g. the probability of germination following gut passage; Schupp et al. 2010).

Seed dispersal distances are a function of seed retention time and movement patterns (Yoshikawa et al. 2019) and form the dispersal kernel, which is a probability density function describing the distribution of dispersal distances relative to the parent plant, i.e. how far a seed will be dispersed (Nathan et al. 2012). Dispersal away from the parent can reduce density-dependent mortality of seedlings and mortality due to natural enemies and seed predators (Janzen 1970; Connell 1971), thus, seed retention time is a quality component of seed dispersal effectiveness. Although lizards move shorter distances than birds and mammals per unit time, gut passage times in reptiles are much longer (several days compared to several minutes/ hours) due to their physiology (Castilla 2000). Longer gut passage times may affect germination success, with success declining with longer seed retention times reported in some studies (Murray et al. 1994; Rodríguez-Pérez et al. 2012), but not others (Castilla 2000).

There are few studies of seed retention time in reptiles globally, with only two unpublished studies for New Zealand species (B. Goetz pers. comm. cited in Whitaker 1987; Lawrence 1997 cited in Wotton et al. 2016). To add to the limited knowledge on lizard seed dispersal in New Zealand, particularly the lack of seed retention times, we investigated seed retention time in *Hoplodactylus duvaucelii*. We evaluated the relationship between body mass and seed retention time to assess the appropriateness of using allometric scaling to apply the results to other New Zealand lizard species.

Methods

Study species

Hoplodactylus duvaucelii (Duvaucel's gecko) is the largest gecko species in New Zealand, with a maximum body weight of 118 g and a maximum snout-to-vent length of 160mm

(Meiri 2008; van Winkel et al. 2018). *H. duvaucelii* are confined to offshore islands on the east coast of the North Island, islands in the Cook Strait, and mainland fenced sanctuaries (Department of Conservation 2022). Their conservation status is At Risk – Relict, with previous mainland populations now extinct (Hitchmough et al. 2021). *H. duvaucelii* have been recorded eating *Piper excelsum* and *Coprosma* spp. on the Poor Knights and Mercury Islands (Whitaker 1987), but their current and past contribution to seed dispersal is unknown.

Seed retention trials

We conducted two seed retention trials with *H. duvaucelii* at the Massey University Reptile Breeding Facility, taking advantage of the quarantine period prior to the geckos translocation. The geckos were housed in individual enclosures with access to food, water, and shelter, and were kept in 12-hour daylength. The temperature in the room varied, so a Kestrel 5500 Weather Meter was used for the duration of the experiment to record temperature hourly. In the first trial in February/March, the mean temperature was 22.7 °C and ranged from 19.5 °C to 24.2 °C; and in the second trial in November/December, the mean temperature was 20.5 °C (16.7–24.2°C).

The first seed retention trial was conducted from 13 February to 16 March 2020, using 44 individuals. All geckos were adults (≥ three years old, 50–90 grams) and not known to be pregnant. There were 27 males and 17 females, and a normal body mass distribution (70.9 g ± 7.9; mean ± 1 SD). Fruits were collected from at least three individuals of the focal species and stored in a fridge until the start of the trial (*Melicytus ramiflorus, Coprosma robusta, Piper excelsum, Corokia cotoneaster, Myoporum laetum, Cordyline australis,* and *Muehlenbeckia astonii*). The fruit was ripe at the time of the study and considered attractive to lizards (Wotton et al. 2016). Fruits were stored for a maximum of two weeks before use in the trial, and only ripe fruits were offered.

On 13 February, after not eating for three days (their usual feeding interval), 14 individuals were each given ten *M. ramiflorus* fruits. We did not force feed the lizards as we wanted to see which fruits they would willingly consume. Each gecko was checked every two hours to estimate consumption time. The following morning, uneaten fruits were removed, and regular feeding (invertebrates and fruit paste without seeds) resumed. Each gecko was checked every two hours from 9 am to 11 pm, with any scats removed and visually examined for the presence of seeds. Checks every two hours continued for five days, followed by twice daily for the next week (every 12 hours), and once daily until 16 March. On 17 February, an additional 28 individuals were given either ten *C. robusta* fruits or one-half of a *P. excelsum* fruit, and on 21 February, 28 individuals were given either ten fruits of *C. australis, M. astonii, M. laetum, C. cotoneaster,* or *M. ramiflorus*. We used the same procedures as the initial trial. Some individuals in the trial on 21 February that had defecated seeds were resampled but were unlikely to have retained seeds in their guts eight days (192 hours) after the first trial.

A second seed retention trial was undertaken from 30 November to 7 December 2020, using 34 geckos in quarantine prior to translocation. The geckos sampled were different individuals to the first trial. There was a limited range of individual body sizes and sex, with 23 adults over 50 g (20 females and three males) and 11 juveniles under 25g (55.8 g ± 26.5; mean ± 1 SD). The juveniles could not be sexed. Due to the study occurring before peak fruiting season (January–April), the only native fruit available was *P. excelsum*. Thus, strawberries (*Fragaria* sp.), blueberries (*Vaccinium* sp.), and gold kiwifruit (*Actinidia chinensis*) were also offered to the geckos. The geckos had not eaten for three days prior to the experiment, and on 30 November, 32 geckos were given either one-half of a *P. excelsum* fruit, two *Vaccinium* sp. fruits cut in half, or three slices of *Fragaria* sp. Thirteen geckos that had not consumed fruits were offered one slice of *Actinidia chinensis* and two *Vaccinium* sp. fruits on 1 December. These geckos were given their usual diet on 31 November, as they had not eaten for four days. Not enough ripe *P. excelsum* could be collected for subsequent feedings. The same procedure for the previous trials was used, and all geckos were checked until all individuals had defecated seeds on 7 December.

Statistical analysis

The geckos were not continuously monitored, so the seed retention times represent maximum and minimum times, and both were calculated for each individual as one minute after the last check before ingestion record and one minute before the defecation record (maximum); and one minute before the ingestion record and one minute after the last check before defecation record (minimum). The retention time for each individual gecko was calculated as the mid-point of these minimum and maximum seed retention times, and grand means of mid-points were calculated across all individuals classified by sex and plant species. Seed masses for native species were taken from Burrows (1996) and Moles et al. (2000) and non-native seeds were air dried and weighed (Appendix S1 in Supplementary Material). A chi-squared test of independence with Yate's correction was used to assess the relationship between fruit species offered to the geckos and the proportion of geckos that ate them. A two-sample *t*-test was used to test the difference in seed retention between males and females, between adults and juveniles, and between native and non-native fruits. ANOVA was used to test for seed retention time differences between fruit species followed by pairwise species comparisons with Tukey adjustment. Linear regression models were used to test if seed retention time was predicted by adult gecko body mass, or seed mass and biogeographic origin (native or non-native fruit species) and the interaction between seed mass and origin. No individual geckos consumed fruits more than once, so mixed effects models were not used. All analyses were carried out using R version 4.2.2 (R Core Team 2022).

Results

Fruit preferences

The proportion of lizards that ate fruits differed among fruit species ($X^2 = 90.7$, d.f. = 9, $P < 0.0001$). *P. excelsum* was the fruit consumed by the highest proportion of individual geckos that were offered it, followed by *M. astonii* and *Fragaria* sp. (Table 1). Few individuals consumed *Vaccinium* sp., *C. robusta, A. chinensis* and *M. ramiflorus*, and none consumed *C. australis, C. cotoneaster,* and *M. laetum* (Table 1).

Seed retention time

Three geckos that consumed fruits gave birth, so they were removed from the study. Fifty-one of 75 (68%) individual geckos consumed fruits (not including the three gravid individuals). Seeds were only recovered from 41 of these

Table 1. Number of geckos that ate each fruit species.

Fruit Species	No. of geckos sampled	No. of geckos ate fruit
Piper excelsum	22	22
Muehlenbeckia astonii	13	11
Fragaria sp.	11	8
Vaccinium sp.	11	2
Coprosma robusta	13	2
Actinidia chinensis	13	2
Melicytus ramiflorus	27	3
Corokia cotoneaster	11	0
Myoporum laetum	11	0
Cordyline australis	11	0

individuals, with many geckos in the first trial not giving any recovered seeds. Scats were collected and examined for seeds for three weeks after seed ingestion, which is significantly longer than the expected seed retention time of four days (101 hours) for a 90 g reptile ($3.429 + 0.181 \times \log_{10} mass$; in Yoshikawa et al. 2019). The enclosures could have been cleaned by facility staff by mistake and scats removed, or the seeds destroyed in the gut passage; however, no seed fragments were found in these scats.

In the initial trial with just *M. ramiflorus*, only two geckos (both females) consumed any fruits, both with very short median seed retention times (13 and 22 hours; Fig. 1). These geckos had only been in quarantine for a few days, and the rapid retention times were likely due to stress; thus, these two records were removed from subsequent analysis. The mean seed retention time for all geckos was 69.2 ± 4.4 hours, ranging from 30.8 to 144.7 hours (one to six days). There was no significant

difference between the mean seed retention time in males and females (mean $\pm$ 1 SEM throughout; 74.4 ± 6.0 hours. 76.7 ± 8.0 respectively ($t_{(29)} = 0.231$, $P = 0.817$). Juveniles had a shorter mean seed retention time (44.5 ± 3.6 hours) than adults (75.6 ± 4.89 hours ($t(41) = -3.15$, $P = 0.003$). There was no relationship between adult body mass and seed retention time ($r^2 = 0.021$, $P = 0.437$, $F_{1,29} = 0.630$; Fig. 1).

Mean seed retention time differed among plant species, ($F_{(6, 32)} = 3.13$, $P = 0.015$; Fig. 2). Seed retention time was highest for *P. excelsum* and lowest in *Fragaria* sp. ($t_{(32)} = 3.30$, $p = 0.034$), but there was no difference between other species. Seed retention time was not affected by seed mass, but non-native fruits were retained for significantly shorter times than native fruits ($r^2 = 0.2831$, $P = 0.009$, $F_{3.35} = 6.002$) (Table 2).

Discussion

Although New Zealand lizards are known to disperse seeds of many plant species, there are few species-specific estimates of seed retention time. Global syntheses have suggested that due to their metabolism, lizards may retain seeds for long periods (Yoshikawa et al. 2019). The mean seed retention time in our study of *H. duvaucelii* was 69 hours and was (1) significantly shorter in juveniles than adults, and (2) longer for native than non-native fruit species. This mean retention time is similar to predictions from allometric models and experimental data for lizards of 7–72 g, which report mean seed retention times of 43 to 99 hours (Yoshikawa et al. 2019; Yang et al. 2021). The difference between juvenile and adult individuals suggests that ontogenetic changes, including mass and behaviour, may be important in predicting retention time. Few studies have examined intra-species mass effects on seed retention time in lizards; however, McConnachie and Alexander (2004) found mass to positively predict gut passage time in *Pseudocordylus*
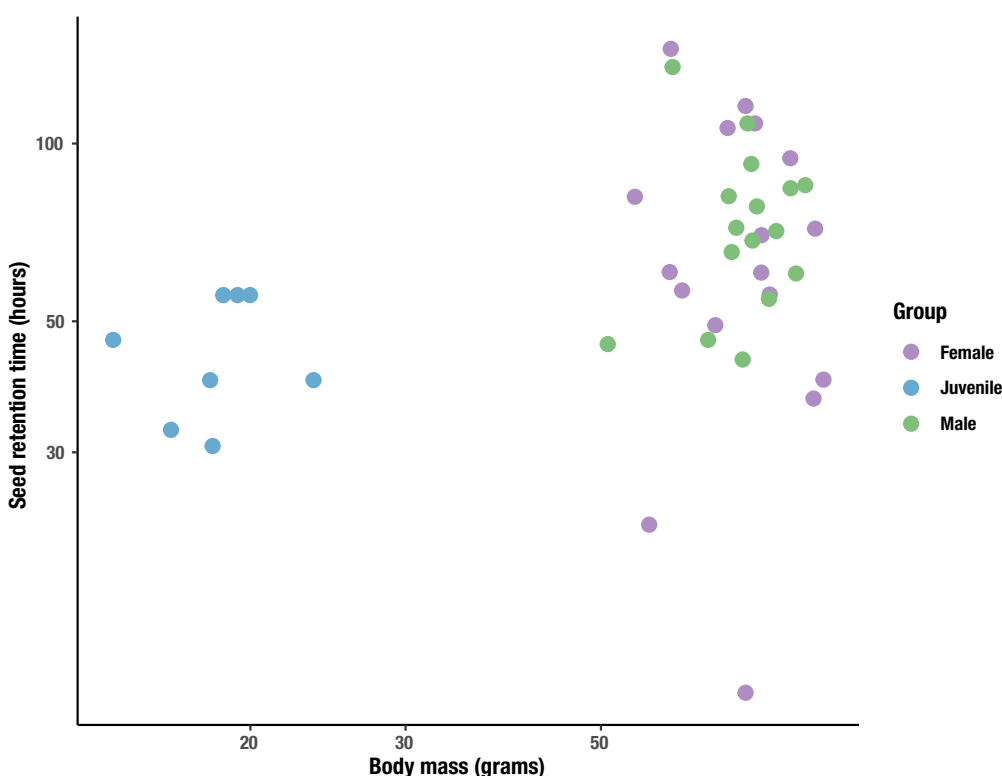

Figure 1. Seed retention time (midpoint, hours) as a function of body mass (grams) in 41 Duvaucel's geckos. Seeds ingested were *Melicytus ramiflorus*, *Coprosma robusta*, *Piper excelsum*, *Muehlenbeckia astonii*, *Fragaria* sp., *Actinidia chinensis*, and *Vaccinium* sp.
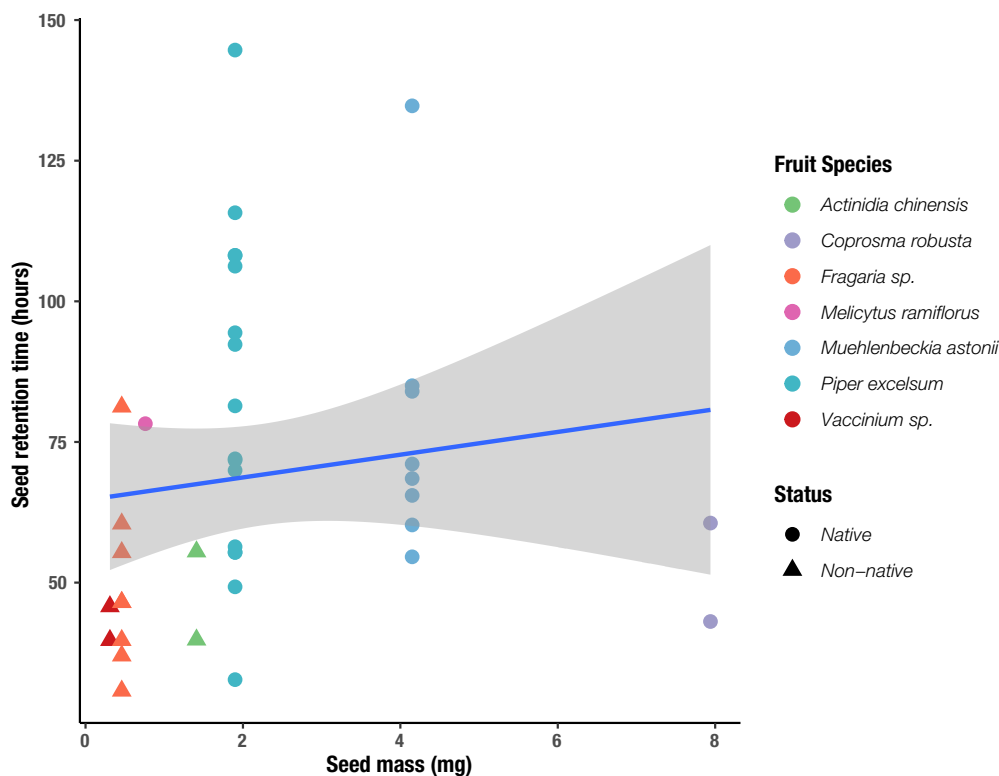
Figure 2. Linear model of the relationship between seed retention time (midpoint, hours) and seed mass (milligrams) for fruits consumed by 39 Duvaucel's geckos. Note two *M. ramiflorus* records have been omitted. Shaded area represents 95% confidence interval.

Table 2. Estimated seed retention times (hours) for New Zealand lizards.

Species	Weight range (adults)	Average daily movement	Estimated retention time (Yoshikawa et al. 2019)
H. duvaucelii	50–118 grams	9.85 metres	101 hours
O. otagense	28–45 grams	12 metres	89 hours
O. waimatense	14–28 grams	11 metres	82 hours
M. "Southern NI"	14–20 grams	9.5 metres	77 hours

melanotus (common crag lizard) but only at 22 °C (other trials were conducted at 20, 25, 30, 32, and 35 °C).

Reptiles are ectothermic, and thus their gut passage time is influenced by the environmental temperatures they experience, further obscuring possible body-mass effects. At lower temperatures, metabolism is slowed, reducing gut passage time. Yoshikawa et al. (2019) reviewed seed retention times for all vertebrate groups and found a general increase with body mass, but for reptiles, the minimum seed retention time was longer and less correlated with body mass. Other studies have reported that higher temperatures decrease gut passage time in lizards (e.g. Van Damme et al. 1991; McConnachie & Alexander 2004). A New Zealand gecko, *Woodworthia* "Southern Alps" had shorter seed retention times at higher temperatures, with 11 days at 10 °C, two days at 17 °C, and one day at 20 °C (Lawrence 1997). The plant species tested by Lawrence (1997) were *Melicytus alpinus*, *Acrothamnus colensoi*, *Leucopogon fraseri*, and *Coprosma petriei*. Another New Zealand native gecko, *Woodworthia maculata*, had seed retention times between one and a half days to three days at an unknown temperature using unknown plant species (B. Goetz pers. comm. cited in Whitaker 1987).

Male and female geckos did not differ in seed retention times, which is consistent with previous studies of lizard seed retention times (Castilla 2000; Santamaría et al. 2007; Rodríguez-Pérez et al. 2012). Seed retention time of non-native fruits was significantly shorter than native fruits, but this was not explained by seed mass. Rodríguez-Pérez et al. (2012) reported no relationship between seed retention time and seed mass in *Podarcis lilfordi* (Lilford's wall lizard). Further investigation into the digestive ecology of native lizards is needed before conclusions about the decreased seed retention time in non-native plant species can be made.

Movement data is lacking for New Zealand lizards, especially for smaller species (< 10 g) and for skinks, but van Winkel (2008) found *H. duvaucelii* average movement distance was 9.85 m per day, with distances up to 50 m per day. Another frugivorous New Zealand lizard, *Oligosoma otagense* (28–45 g) averaged 12 m per day (Germano 2007). Even smaller New Zealand lizards such as *Oligosoma waimatense* (14–28 g) move an average of 11 m per day (Lettink & Monks 2019), and *Mokopirirakau* "Southern North Island" (14–20 g) move an average of 9.5 m per day (Romijn et al. 2014). The allometric models presented in Yoshikawa et al. (2019) enable us to predict seed retention times for these species (Table 2).

These estimates, along with our mean of 69 hours for

Duvaucel's geckos, suggest that lizards with body mass of at least 14 g could easily disperse seeds over 10 m from the parent plant during their seed retention window, allowing seeds to escape the effects of density-dependent seedling mortality, natural enemies, and seed predators (Janzen 1970; Connell 1971). However, behavioural ecology is also crucial, with extreme sit and wait predators such as *Naultinus* spp. having shorter movement distances (Hare et al. 2007; Knox & Monks 2014; Knox et al. 2017). Lizards may also have longer seed retention times in cooler temperatures; however, this could be negated by the reduction in food intake (i.e. fewer fruits ingested) and movement activity (Barry et al. 2010), and a reduction in available fruit during winter.

The dispersal of seeds away from their parent plant is just one component of seed dispersal effectiveness, as post-dispersal, seeds must germinate and survive (Schupp et al. 2010). Passage through a vertebrates' gut can influence germination by removing the fruit pulp from the seed (deinhibition), which can reduce germination inhibitors and alter the seeds microenvironment; and by scarification of the seed, which may alter the seed coat (Samuels & Levey 2005; Robertson et al. 2006). Determining the effect of gut passage on germination is difficult as most studies only test the effect of scarification and use different metrics of germination success (e.g. rate, percentage, and seedling survival) (Robertson et al. 2006). Studies of scarification and deinhibition by reptiles have not shown consistent effects on any of these metrics (Wotton 2002; Santamaría et al. 2007; Rodríguez-Pérez & Traveset 2010; Zuël et al. 2012; Wotton et al. 2016). Future studies examining the outcomes of deinhibition and scarification on germination and seedling survival following consumption by New Zealand lizards are necessary to determine if they are effective seed dispersers.

Our study provides the first estimates of seed retention time and seed dispersal potential for *H. duvaucelii*, which retained seeds for 31 to 145 hours (one to six days), suggesting they could move seeds at least 10 m away from parent plants. Body mass did not predict seed retention time which may be due to thermoregulation. Future studies could combine seed retention times with movement data to estimate seed dispersal kernels for many New Zealand lizards.

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Additional Information and Declarations

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Seed sizes and number of seeds of fruits offered to geckos.

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