

Seed retention times in the New Zealand pigeon (*Hemiphaga novaeseelandiae novaeseelandiae*)

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Abstract: We offered ripe fruits of tawa (*Beilschmiedia tawa*), taraire (*B. tarairi*), and pūriri (*Vitex lucens*) to captive New Zealand pigeons (*Hemiphaga novaeseelandiae*) and recorded seed retention times. We also recorded seed retention times while radio-tracking wild pigeons in Taranaki and Canterbury. We report wild pigeon retention times for tawa, pūriri, miro (*Prumnopitys ferruginea*), fivefinger (*Pseudopanax arboreus*), and kahikatea (*Dacrydium dacrydioides*) seeds. Where data were available for the same plant species from wild and captive pigeons, retention times were similar. Seed retention time differed significantly among fruit species, and was positively related to seed mass. Mean retention times ranged from 37–45 min for the two smallest-seeded species (fivefinger and kahikatea) up to 109–181 min for the three largest species (pūriri, taraire, and tawa). We also report the second published instance of regurgitation by the New Zealand pigeon.

Keywords: frugivory; kererū; regurgitation; seed dispersal; seed size

Introduction

Internal transport of fleshy fruits by avian frugivores is a widespread seed dispersal mechanism (Howe & Smallwood 1982). Frugivorous birds and fruiting plants both encounter a range of trade-offs relating to the length of time dispersers retain seeds after ingesting fruits. The treatment of seeds by animal dispersers can have important consequences for plant reproductive success. From the plant's perspective, seed retention time is a trade-off between dispersal distance and seed viability (Murray et al. 1994). Longer seed retention times generally result in greater dispersal distances (Murray et al. 1994; Holbrook & Smith 2000), but decreased seed viability (Murphy et al. 1993; Murray et al. 1994; Charalambidou et al. 2003). For animal frugivores, seed retention time is a trade-off between absorbing nutrients from the fruit pulp and eliminating the indigestible seed 'ballast' (Snow 1971; Levey & Grajal 1991). The presence of seeds in a bird's gut limits its capacity for food ingestion (Sorensen 1984). In addition, the weight of seeds increases the energy expenditure required for flight (Levey & Grajal 1991).

In the New Zealand flora around 70% of trees, 48% of all woody plants (Burrows 1994), and 12% of all plant species (Lord et al. 2002) have fleshy fruits that rely on animals for dispersal. The only native terrestrial mammals in New Zealand are one extinct and two threatened

species of Microchiropteran bat, which may play a (now very limited) role in dispersal of small-seeded species (Lord et al. 2002). Lizards disperse small fleshy fruits in New Zealand (Whitaker 1987; Wotton 2002), but most fleshy-fruited species are bird-dispersed. The New Zealand pigeon, kererū (*Hemiphaga novaeseelandiae novaeseelandiae* Gmelin, Columbidae) is a large (c. 650 g; Clout & Tilley 1992), frugivorous pigeon widespread throughout New Zealand (Clout & Hay 1989). The New Zealand pigeon plays an important seed dispersal role, consuming fruits of at least 70 plant species and defecating the seeds intact (McEwen 1978; Clout & Hay 1989; Kelly et al. 2006). It is the largest extant native frugivore, and the only resident bird easily able to swallow fruits over 14 mm diameter, which are produced by five native trees (Clout & Hay 1989). The only published seed retention times in the New Zealand pigeon give a mean of 95 min for miro (*Prumnopitys ferruginea* (D. Don) de Laub., Podocarpaceae) (Clout & Tilley 1992). Our research aimed to answer the following questions:

- (1) How long does it take for seeds of a range of native species to pass through the gut of New Zealand pigeons?
- (2) Do seed retention times for New Zealand pigeons vary among plant species?
- (3) Is seed retention time related to seed size?

Materials and methods

Study sites

We conducted seed passage trials with captive New Zealand pigeons in outdoor aviaries at Orana Wildlife Park (43°28' S, 172°28' E) and Willowbank Wildlife Reserve (43°28' S, 172°36' E), in Christchurch, New Zealand. The aviaries were large enough for pigeons to undertake short flights, with the exception of one injured individual, which was unable to fly and was held separately in a smaller aviary. Captive pigeons were maintained on a diet of sweet corn, peas, commercially available fruit (e.g. kiwifruit, *Actinidia deliciosa*), bread, and seeds. Maintenance food for the pigeons was placed in the aviaries once a day, usually around mid-morning.

We radio-tracked wild pigeons in Taranaki and on Banks Peninsula, Canterbury, New Zealand, which had been radio-tagged for other studies (Campbell 2006; R.G. Powlesland, Department of Conservation, Wellington, New Zealand, pers. comm.). Pigeons in Taranaki were located in and around New Plymouth city (39°04' S, 174°05' E) in native forest remnants and in urban parks with mixed native and introduced vegetation. On Banks Peninsula, pigeons were mostly tracked in Hinewai Reserve (43°49' S, 173°02' E) and on adjacent farmland. Hinewai covers 1000 ha of mostly early-successional native forest (Wilson 1994). One individual was tracked in the nearby township of Akaroa (4 km east of Hinewai).

Captive trials

We offered captive pigeons native fruits of three species: tawa (*Beilschmiedia tawa* (A.Cunn.) Benth. et Hook. f. ex Kirk, Lauraceae), taraire (*B. tarairi* (A.Cunn.) Benth. et Hook. f. ex Kirk), and pūriri (*Vitex lucens* Kirk, Verbenaceae), all of which are important in the diet of wild pigeons (McEwen 1978). Both tawa and taraire have large, dark purple to black fleshy fruits with a single seed. Tawa fruits are c. 27 × 16 mm containing a single seed c. 24 × 12 mm (length × diameter; Wotton & Ladley in press). Taraire fruits are larger than tawa, measuring c. 32 × 19 mm with a single seed 29 × 16 mm (Wotton & Ladley in press). Pūriri has pinkish red, fleshy fruits measuring 18 × 16 mm (J.M. Lord, University of Otago, Dunedin, New Zealand, pers. comm.). The dispersal unit of pūriri (for convenience hereafter referred to as a seed) consists of between one to four seeds enclosed in a ridged woody endocarp about 14 mm long, which remains intact after ingestion (Godley 1971; Webb & Simpson 2001). Taraire and pūriri fruits were collected in July 2006 from Wenderholm Regional Park (36°32' S, 174°42' E), near Auckland, New Zealand, and tawa fruits were collected in April 2006 from Blue Duck Reserve, Kaikoura, New Zealand (42°14' S, 173°47' E).

We offered fruits of the three species in separate trials once or twice to each individual pigeon. Fruits were

offered to 10 pigeons, although only five pigeons in total (two males, two females and one of unknown sex) actually ingested fruits. Twenty fruits of a single species were placed in the usual feeding tray in the aviary in the morning before normal food was made available. We recorded the times at which fruits were eaten and the number of fruits eaten. Any fruits not consumed within 10 min of the first fruit being swallowed were removed in order to keep the range of ingestion times small for seeds in one feeding bout, and the normal food supply was placed in the feeding tray. We observed pigeons continuously until all seeds were recovered, recording the time of each defecation and the number of seeds defecated. We use the term 'seed retention' to encompass both seeds that were defecated and those that were regurgitated. 'Seed passage' refers only to those seeds that were defecated. We calculated seed retention times by subtracting the midpoint of the time between ingestion of the first and last fruits from the time of egestion.

Wild seed passage times

We collected data on seed passage times while radio-tracking wild pigeons from January to April 2006. Pigeons were fitted with Sirtrack radio-transmitters and located using Sirtrack TR4 and R1000 receivers and 160 MHz folding Yagi antennae (Sirtrack, Havelock North, NZ). We tracked individual pigeons continuously from early morning for up to 8.5 h. During each tracking session we recorded the time of feeding observations, noting the species of any fruit consumed. We also recorded the time of any defecations containing seeds, and when these could be collected identified the seeds to species. We collected defecations from four male birds in Taranaki, and one of unknown sex in Akaroa. We determined seed passage times only for those observations that met the following criteria: (1) pigeons defecated seeds after the first observed feeding on a fruit species for that day and before repeated feeding on the same species; or (2) there was a minimum 5-h interval between the feeding observation and any prior ingestion of fruit of the same species, and no repeated feeding was observed on the same species before seed defecation. Note that this introduces a bias, because passage times from the first feeding bout in a day are truncated (upper limit on passage time) when the bird has a second feeding bout on the same plant. Because birds were very sedentary, we consider this bias will not greatly skew the results, but it must be considered. We calculated seed passage times by subtracting the time at the midpoint of the feeding bout from the time of defecation (Murray 1988).

Data analysis

For captive trials we tested for differences in seed retention time between fruit species, using a two-tailed ANOVA. For pūriri we were able to test the difference in retention times between wild versus captive pigeons using a two-

sample *t*-test, in case differences in activity levels of the birds affect retention times (see Discussion). For fruit species where we had both wild and captive retention times we combined all data for that plant to calculate an overall mean seed retention time, which was used in subsequent analyses. We used a two-tailed ANOVA test for differences in seed retention time between fruit species (wild and captive data combined). We carried out a linear regression to determine whether mean seed retention time was related to mean seed mass across all plant species. In this analysis we included Clout & Tilley's (1992) passage time data for miro seeds in captive pigeons. Air-dried seed mass data were obtained from Moles et al. (2000) for all species except tawa and taraire, for which we collected data from the site at which fruits fed to captive pigeons were collected. We included seeds that were regurgitated in all analyses as there did not appear to be any consistent effect of defecation vs regurgitation on seed retention time, although the number of observations was too small to test this. All analyses were carried out using R version 2.1.1 (R Development Core Team 2005).

Results

Captive trials

Captive pigeons appeared unfamiliar with the native fruits, often dropping fruits repeatedly while attempting to swallow them. The five pigeons that did not ingest any fruits made no attempt to swallow them, showing little interest in the fruits. Tawa fruits were readily ingested by five pigeons, although retention times were recorded for only four individuals. Pigeons appeared to experience considerable difficulty swallowing taraire fruits due to their large diameter. Nevertheless, in the wild New Zealand

pigeons are often observed feeding on taraire fruits.

The number of fruits ingested during a feeding bout appears to be limited by both fruit size and the size of the pigeon's crop. In a single feeding bout with one species of fruit offered, captive pigeons nearly always ingested six or seven pūriri fruits, four tawa fruits, or one taraire fruit (from smallest to largest fruits respectively). Pigeon defecations contained a single seed of tawa or taraire, or between one and three pūriri seeds.

Seed retention times varied significantly among plant species within captive trials ($F_{2,30} = 4.95$, $P = 0.014$). Captive-pigeon retention times ranged from a minimum of 43 min for a pūriri seed to a maximum of 5.5 h for the slowest tawa seeds (Table 1).

We observed two pigeons regurgitate seeds and fruits during captive feeding trials. The first bird ingested four tawa fruits during a single feeding bout, and then regurgitated two partially digested fruits after 57 min and the other two, fully digested, after 5.5 h. This same bird also regurgitated a partially digested taraire fruit after 110 min. The second pigeon regurgitated an intact taraire fruit after 74 min.

Wild seed passage times

We collected seed passage times in wild pigeons for five plant species (Table 1), two of which were also used in captive trials in this study. The number of seeds contained in wild pigeon defecations varied from one seed for tawa, and one to three pūriri seeds, to more than 10 seeds of fivefinger (*Pseudopanax arboreus* (Murray) Philipson, Araliaceae) and kahikatea (*Dacrycarpus dacrydioides* (A.Rich.) de Laub., Podocarpaceae). A single miro seed was collected from a dropping that also contained one pūriri seed. Seed retention times for fivefinger and kahikatea use defecations rather than individual seeds as replicates. Due

Table 1. Seed retention times (min) for native fruits swallowed by captive and wild New Zealand pigeons. The captive data for miro are taken from Clout & Tilley (1992).

Plant species	Common name	Mean	SD	Range	Sample sizes (seeds, defecations, birds)
Captive					
<i>Beilschmiedia tawa</i>	Tawa	180.8	100.3	57–330	15, 13, 4
<i>B. taraire</i>	Taraire	137.8	55.3	74–192	4, 4, 2
<i>Prumnopitys ferruginea</i>	Miro	95.4	25.6	55–140	36, ??, 2
<i>Vitex lucens</i>	Pūriri	91.9	42.3	43–189	14, 11, 2
Wild					
<i>Beilschmiedia tawa</i>	Tawa	254.0	11.3	246–262	2, 2, 1
<i>Vitex lucens</i>	Pūriri	122.4	66.3	63–269	17, 10, 3
<i>Prumnopitys ferruginea</i>	Miro	80.0	–	–	1, 1, 1
<i>Dacrycarpus dacrydioides</i>	Kahikatea	44.5	2.1	43–46	–, 2, 1
<i>Pseudopanax arboreus</i>	Fivefinger	37.4	9.9	19–50	–, 9, 1

to the small seed size for these two species we were unable to recover and count all seeds. Although we recorded wild passage times for only a small number of seeds, these were consistent with times recorded for captive pigeons (Table 1). Pūriri retention times did not differ significantly among captive and wild pigeons (means of 92 and 122 min respectively, $t_{29} = -1.487$, $P = 0.148$). The two tawa seed passage times we collected from wild birds were within the range for our captive birds (Table 1), and the single miro seed passage time of 80 min we recorded in the wild was also comparable to the mean for captive birds of 95.4 min given by Clout & Tilley (1992).

Differences among species

The overall mean seed retention time for pigeons in our data was 120 ± 82 min. Mean seed retention time, combining captive and wild data, was 108.6 ± 57.9 min for pūriri and 189.4 ± 97.0 min for tawa. Seed retention time differed significantly among fruit species across wild and captive samples combined ($F_{5,58} = 7.18$, $P < 0.001$), and was significantly affected by seed mass (Fig. 1; adjusted $R^2 = 0.687$, regression equation = $55.61 + 47.22x$, $F_{1,4} = 11.96$, $P = 0.026$).

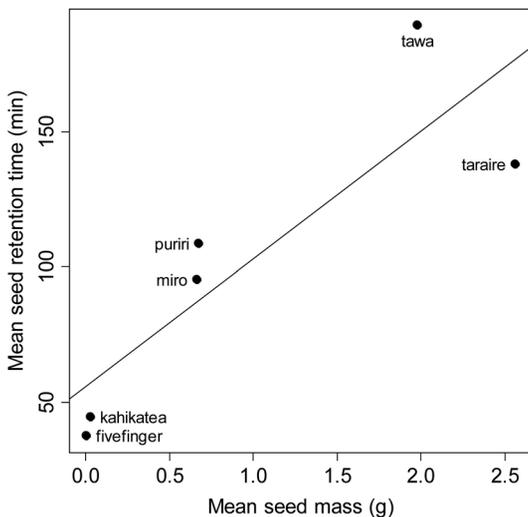


Figure 1. Relationship between mean seed mass and mean seed retention time for six fruit species consumed by wild and captive New Zealand pigeons. Seed mass data are from Moles et al. (2000), except for tawa and taraire measured at our sites. The relationship was significant (see text).

Discussion

Seed retention times are relatively long in New Zealand pigeons compared with other avian frugivores. Small passerines typically defecate seeds within an hour of ingestion (Sorensen 1984; Murphy et al. 1993), and often within 20 min (Levey 1987; French 1996). This contrasts with New Zealand pigeon seed retention times, which range from 19 to 330 min, with an overall mean of 2 h. However, given the large size of New Zealand pigeons our results are consistent with evidence that seed retention time increases with frugivore body size (Herrera 1984; Levey 1986; Holbrook & Smith 2000). As long retention times tend to produce greater dispersal distances, the large size and long retention times of New Zealand pigeons accentuate their importance as dispersers.

The relationship between seed passage time and seed size appears to be inconsistent among avian seed dispersers. Seed passage time in New Zealand pigeons increases with increasing seed size, which agrees with results reported for a number of other studies (Sorensen 1984; Holbrook & Smith 2000; Westcott et al. 2005). However, other authors show either a negative relationship (Levey 1986; Levey & Grajal 1991; Stanley & Lill 2002; Fukui 2003), or no relationship between seed passage time and seed size (Sun et al. 1997). It appears that other characteristics of both fruits and dispersers also influence seed passage time. For example, some birds may process carbohydrate-rich foods more rapidly than lipid-rich ones (Afik & Karasov 1995). Lipids require more time to digest and absorb than simple sugars (Witmer & Van Soest 1998). Specialist frugivores can also have a more rapid gut passage rate than other birds (Herrera 1984).

Frugivores face conflicting demands between retaining fruits for a sufficient period of time to assimilate nutrients and discarding the indigestible seed as rapidly as possible (Murray et al. 1994). Regurgitation is a common method overseas of rapidly processing large seeds, where birds regurgitate large seeds and defecate smaller ones (Johnson et al. 1985; Levey 1986, 1987; McConkey et al. 2004). Nevertheless, we know of only three records of regurgitation in New Zealand: a single pigeon regurgitating a pūriri fruit (McEwen 1978); *Hemiphaga novaeseelandiae chathamensis* Rothschild regurgitating *Myrsine chathamica* F. Muell. (Myrsinaceae) fruits on Chatham Island (R.G. Powlesland pers. comm.); and South Island robins casting pellets containing berry seeds (Powlesland 1979).

Regurgitation may be under-reported as it is difficult to observe in dense forest where pigeons are often found. However, it does not seem to be common, and the New Zealand pigeon does not use regurgitation as a means of rapidly eliminating large seeds. Although there were too few data for formal testing, regurgitation times were comparable to defecation times, and most regurgitated fruits were incompletely digested. Pigeons thus gain little

benefit from regurgitation in terms of rapid seed processing or nutrient assimilation, and may regurgitate fruits only when stressed (McEwen 1978).

Seed passage trials conducted with captive birds have limitations (Holbrook & Smith 2000) because captive birds are likely to be relatively inactive compared with wild ones and seed passage times may therefore be slower. However, feeding by the New Zealand pigeon in the wild is often followed by a long period of inactivity (McEwen 1978; DMW unpubl. data), as also reported for frugivorous birds and bats overseas (Levey & Grajal 1991). We found that seed retention times were similar for wild and captive birds, but this conclusion remains tentative until more data are available. Wild-bird seed retention times are notoriously difficult to measure and there are few previously published estimates (Howe 1977; Howe & Vande Kerckhove 1981; Wheelwright 1991).

In addition, the diet of captive birds may differ considerably from that of wild birds. Individual birds in captivity can modify their gut processing rate in response to changes in diet (Afik & Karasov 1995). The captive diet of the New Zealand pigeons we used differed from that of wild pigeons, although it did include fruit.

Seed dispersal distance is a function of frugivore movement patterns and seed retention times (Westcott et al. 2005). Our results enable estimation of seed dispersal distances by the New Zealand pigeon for a range of plant species, which we will report in a subsequent paper. Meanwhile, it is apparent that seed retention times of up to five and a half hours combined with seasonal movements of tens of kilometres (Clout et al. 1986, 1991) indicate the potential for effective seed dispersal over long distances by the New Zealand pigeon. Such dispersal is increasingly important in conservation terms, for maintaining metapopulation integrity in native forest remnants separated by farmland.

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References

- Afik D, Karasov WH 1995. The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* 76: 2247–2257.
- Burrows CJ 1994. The seeds always know best. *New Zealand Journal of Botany* 32: 349–363.
- Campbell KL 2006. A study of home ranges, movements, diet and habitat use of kereru (*Hemiphaga novaeseelandiae*) in the southeastern sector of Banks Peninsula, New Zealand. Unpublished MSc thesis, Lincoln University, New Zealand. 116 p.
- Charalambidou I, Santamaria L, Langevoord O 2003. Effect of ingestion by five avian dispersers on the retention time, retrieval and germination of *Ruppia maritima* seeds. *Functional Ecology* 17: 747–753.
- Clout MN, Hay JR 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. *New Zealand Journal of Ecology* 12 (Supplement): 27–33.
- Clout MN, Tilley JAV 1992. Germination of miro (*Prumnopitys ferruginea*) seeds after consumption by New Zealand pigeons (*Hemiphaga novaeseelandiae*). *New Zealand Journal of Botany* 30: 25–28.
- Clout MN, Gaze PD, Hay JR, Karl BJ 1986. Habitat use and spring movements of New Zealand pigeons at Lake Rotorua, Nelson Lakes National Park. *Notornis* 33: 37–44.
- Clout MN, Karl BJ, Gaze PD 1991. Seasonal movements of New Zealand pigeons from a lowland forest reserve. *Notornis* 38: 37–47.
- French K 1996. The gut passage rate of Silvereyes and its effect on seed viability. *Corella* 20: 16–19.
- Fukui A 2003. Relationship between seed retention time in bird's gut and fruit characteristics. *Ornithological Science* 2: 41–48.
- Godley EJ 1971. The fruit of *Vitex lucens* (Verbenaceae). *New Zealand Journal of Botany* 9: 561–568.
- Herrera CM 1984. Adaptation to frugivory of Mediterranean avian seed dispersers. *Ecology* 65: 609–617.
- Holbrook KM, Smith TB 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia* 125: 249–257.
- Howe HF 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58: 539–550.
- Howe HF, Smallwood J 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.

- Howe HF, Vande Kerckhove GA 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology* 62: 1093–1106.
- Johnson RA, Willson MF, Thompson JN, Bertin RI 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology* 66: 819–827.
- Kelly D, Robertson AW, Ladley JJ, Anderson SH, McKenzie RJ 2006. The relative (un)importance of introduced animals as pollinators and dispersers of native plants. In: Allen RB, Lee WG eds *Biological invasions in New Zealand*. Ecological Studies 186. Berlin & Heidelberg, Springer. Pp. 227–245.
- Levey DJ 1986. Methods of seed processing by birds and seed deposition patterns. In: Estrada A, Fleming TH eds *Frugivores and seed dispersal*. Dordrecht, Dr W. Junk. Pp. 147–158.
- Levey DJ 1987. Seed size and fruit-handling techniques of avian frugivores. *American Naturalist* 129: 471–485.
- Levey DJ, Grajal A 1991. Evolutionary implications of fruit-processing limitations in cedar waxwings. *American Naturalist* 138: 171–189.
- Lord JM, Markey AS, Marshall J 2002. Have frugivores influenced the evolution of fruit traits in New Zealand? In: Levey DJ, Silva WR, Galletti M eds *Seed dispersal and frugivory: ecology, evolution and conservation*. Wallingford, CABI. Pp. 55–68.
- McConkey KR, Meehan HJ, Drake DR 2004. Seed dispersal by Pacific Pigeons (*Ducula pacifica*) in Tonga, Western Polynesia. *Emu* 104: 369–376.
- McEwen WM 1978. The food of the New Zealand pigeon (*Hemiphaga novaeseelandiae novaeseelandiae*). *New Zealand Journal of Ecology* 1: 99–108.
- Moles AT, Hodson DW, Webb CJ 2000. Seed size and shape and persistence in the soil in the New Zealand flora. *Oikos* 89: 541–545.
- Murphy SR, Reid N, Yan ZG, Venables WN 1993. Differential passage time of mistletoe fruits through the gut of honeyeaters and flowerpeckers: effects on seedling establishment. *Oecologia* 93: 171–176.
- Murray KG 1988. Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs* 58: 271–298.
- Murray KG, Russell S, Picone CM, Winnett-Murray K, Sherwood W, Kuhlmann ML 1994. Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. *Ecology* 75: 989–994.
- Powlesland RG 1979. Pellet casting by South Island robins. *Notornis* 26: 273–278.
- R Development Core Team 2005. R: A language and environment for statistical computing. Version 2.1.1. Vienna, Austria, R Foundation for Statistical Computing.
- Snow DW 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113: 194–202.
- Sorensen AE 1984. Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). *Journal of Animal Ecology* 53: 545–557.
- Stanley MC, Lill A 2002. Does seed packaging influence fruit consumption and seed passage in an avian frugivore? *Condor* 104: 136–145.
- Sun C, Ives AR, Kraeuter HJ, Moermond TC 1997. Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia* 112: 94–103.
- Webb CJ, Simpson MJA 2001. *Seeds of New Zealand gymnosperms and dicotyledons*. Christchurch, Manuka Press and Caxton Press. 428 p.
- Westcott DA, Bentrupperbäumer J, Bradford MG, McKeown A 2005. Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia* 146: 57–67.
- Wheelwright NT 1991. How long do fruit-eating birds stay in the plants where they feed? *Biotropica* 23: 29–40.
- Whitaker AH 1987. The roles of lizards in New Zealand plant reproductive strategies. *New Zealand Journal of Botany* 25: 315–328.
- Wilson HD 1994. Regeneration of native forest on Hinewai Reserve, Banks Peninsula. *New Zealand Journal of Botany* 32: 373–383.
- Witmer MC, Van Soest PJ 1998. Contrasting digestive strategies of fruit-eating birds. *Functional Ecology* 12: 728–741.
- Wotton DM 2002. Effectiveness of the common gecko (*Hoplodactylus maculatus*) as a seed disperser on Mana Island, New Zealand. *New Zealand Journal of Botany* 40: 639–647.
- Wotton DM, Ladley JJ 2008. Fruit size preference in the New Zealand pigeon (*Hemiphaga novaeseelandiae*). *Austral Ecology* 33(3): 341–347.

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