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THE GUT PASSAGE RATE OF SILVEREYES AND ITS EFFECT ON SEED VIABILITY

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The gut passage rate of Silvereyes *Zosterops lateralis,* was measured with fruits of *Coprosma quadrifida*. The rate of passage of seeds was measured when fed to birds whose guts were empty and compared to the rate when fed to birds that had eaten previously. Gut passage rates ranged from six to 28 minutes but was significantly slower when birds had consumed food.

The viability of the ingested seeds was measured using tetrazolium. There was no significant difference in the viability of seeds that had passed through an empty gut versus a gut with food. However, the viability of seeds that had passed through Silvereyes was significantly lower than the viability of fresh seeds.

This study has shown that food availability will influence the speed of passage through the gut and therefore the distance seeds are dispersed. It also suggests that laboratory trials that use starved birds can give erroneous speeds. Although there was little evidence that time spent in the gut affected viability, passage through the gut was clearly disadvantageous for seed viability. However, this may be counteracted by advantages in dispersal distance.

INTRODUCTION

Seeds dispersed by vertebrates often travel through the gut of the vertebrate, an environment that is naturally lethal to the embryo within the seed (Janzen 1983). The viability of the embryo after transit is likely to be influenced by the protective coating surrounding the seed and the length of time the seeds are exposed to the digestive secretions of the gut. Studies on the effect on germination of passage through the gut have sometimes shown enhanced germination and at other times reduced or no effect on germination (Krefting and Roe 1949; Noble 1975; Stocker and Irvine 1983; Lieberman and Lieberman 1986; Barnea *et al.* 1990; Izhaki and Safriel 1990). If seeds do not germinate it is difficult to distinguish between chemical destruction of the embryo in the gut and seed dormancy. Tetrazolium is a chemical that stains respiring tissue red. It is used to test the presence of viable tissue within seeds (Moore 1973) and can therefore measure viability of the seeds directly.

The time for food to pass through the gut is significantly shorter for frugivorous birds than for non-frugivores (Herrera 1984), but some species of birds have been shown to differ in gut passage times depending on the species of fruit (Holthuijzen and Adkisson 1984; Sorensen 1984). Some studies have used birds deprived of food (Holthuijzen and Adkisson 1984; Sorensen 1984; Johnson *et al.* 1985) which may produce divergent results from birds allowed prior access to food, the more common condition for wild birds. Differences in the time spent in the gut may have an important impact on the number of viable seeds that are passed by a species. In laboratory trials, it is therefore important to establish the effect of gut condition on both speed of passage and seed viability so that the relationship with the natural condition is mimicked more closely.

Silvereyes *Zosterops lateralis* are small (9–13 g) frugivores commonly found in many habitats (Blakers *et al.* 1984). They are seed dispersers of both native and introduced plants (Gannon 1936; Liddy 1985; French 1990) and a frequent visitor to the native shrub, *Coprosma quadrifida*, in wet sclerophyll forest in south-eastern Australia (French *et al.* 1992).

The aims of this study were 1) to determine the speed of passage of seeds of *Coprosma quadrifida* through Silvereyes; 2) to assess the effects of gut passage rate on seed viability, and 3) to determine the effect of stomach fullness on passage rate and seed viability.

METHODS

Ten Silvereyes were wild-caught, housed in an outdoor aviary and fed on bird cake and commercially available fruit. The birds were allowed to acclimatize to aviary conditions before experimental trials began.

Measurements of gut passage time (GPT) were performed at first light. Birds were taken from the aviary the evening before and housed in individual cages in the laboratory overnight. The GPT of each bird was measured on two separate mornings. On one morning the birds had empty stomachs, i.e. they had been provided only with water overnight. On the other morning the birds had full stomachs, i.e. they had been provided with birdcake and observed to eat prior to the experiment. The order in which birds received each treatment was randomized.

To measure GPT, birds were provided with 10 *Coprosma quadrifida* fruits and the time was measured from ingestion of the first fruit to the defecation of the first seed. Birds were viewed from behind a one-way window. The seeds were collected when the birds stopped feeding and most of the seeds had been passed.

To test for viability of seeds, seeds were cut in half longitudinally and soaked in 0.1 per cent tetrazolium solution in phosphate buffer (0.5M) for approximately 15 hours (Moore 1973). After treatment, seeds were classified as alive if all or most of the embryo was bright pink, or dead if the embryo was white, mottled or pale pink.

The viability of seeds that had not passed through Silvereyes was determined in seven trials of 20 seeds from randomly chosen fruits. These fresh seeds were tested with tetrazolium in a similar way to seeds that had passed through birds.

Paired *t* tests were used to test for differences in the speed of passage of seeds through full and empty guts. A generalized linear model was used to test for differences in viability of seeds between treatments. For this, a logistic regression equation was modelled. This analysis was used in preference to the paired *t* test as the number of seeds obtained from birds varied greatly and would violate the assumptions of the paired *t* test. Finally, a *t* test was used to test for differences in viability of fresh seed and seed that had passed through birds.

RESULTS

This study showed that GPT was affected by the presence of food in the gut, although GPT was extremely fast in both treatments: GPT ranged from six to 28 minutes. GPT was faster for birds with empty stomachs (mean = 11.8 ± 1.4 (SE) min) than those with full stomachs (mean = 18.0 ± 1.9 min) (paired $t = 2.65$, df = 9, $p = 0.0132$, Fig. 1). This suggests that experiments which starve birds prior to experimentation may be overestimating the speed at which seed moves through the gut through most of the day.

All seeds collected from birds were physically undamaged and often still enclosed in skin from the fruit. No difference was found in the proportion of live seeds between full (0.36 ± 0.04) and empty (0.42 ± 0.06) stomachs in the tetrazolium tests

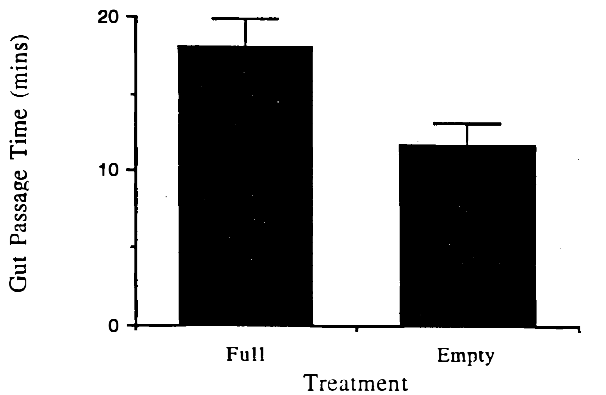

Figure 1. *Mean gut passage time (minutes) of* Coprosma quadrifida *seeds for Silvereyes whose guts were empty (Empty) and for Silvereyes that had eaten previously (Full). Error bars are standard errors. Ten birds were used in each trial.*

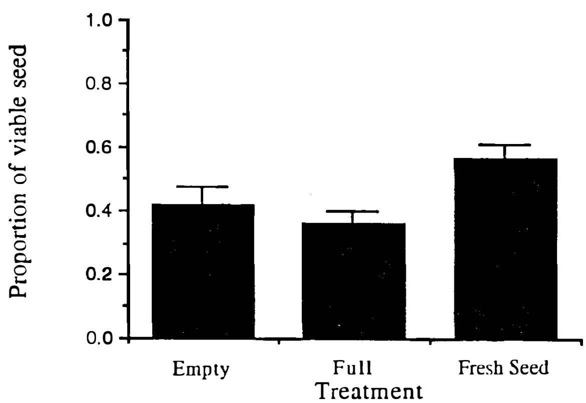

Figure 2. *The mean proportion of viable* Coprosma quadrifida *seeds in samples taken from Silvereyes whose guts were empty (Empty) and for Silvereyes that had eaten previously (Full) and for samples of fresh seed. Error bars are standard errors. Ten birds were used in the Full and Empty trials. Seven samples of fresh seed were analysed.*

($F_{(1,9)}$ = 0.24, p = 0.64, Fig. 2). This indicates that for Silvereyes, the time spent in the gut does not negatively affect seed viability. These results were then pooled for each bird and compared to the proportion of seed alive in the samples of fresh seeds that had not been ingested. The viability of the fresh seeds was significantly higher than seeds that had been through birds (t = 4.30, p = 0.0006, Fig. 2) suggesting that viability is affected by passage through a Silvereye. For fresh seeds 57.1 ± 4.1 per cent of seeds were viable but only 39.3 ± 3.7 per cent were viable after transit through the gut.

DISCUSSION

Silvereyes pass *Coprosma quadrifida* seeds very quickly. A rapid GPT is likely to be related to three factors. Firstly, speed of passage is linked to the size of the bird (Herrera 1984): smaller birds have faster GPTs. Secondly, frugivorous birds have faster GPTs than non-frugivorous birds (Herrera 1984). For these the gut is often shorter and simpler, and indigestible material is preferentially moved through quickly. Thirdly, fruit may have a laxative effect reducing GPT. Rapid GPTs have been recorded for a number of other frugivorous species. Phainopeplas *Phainopepla nitens* pass seeds in 12–45 minutes (Walsberg 1975), Cedar Waxwings *Bombycilla cedrorum* in 12–23 minutes (Holthuijzen and Adkisson 1984), Bulbuls *Pycnonotus xanthopygos* in 4.8–5.6 minutes and Blackbirds *Turdus merula* in 4.5 minutes (Barnea *et al.* 1990). The transit times for native seeds through the gut has rarely been measured for birds in Australia (but see Willson 1989 for Emus, *Dromaius novaehollandiae*) and little information has been provided on the viability of these seeds except after passage through Cassowaries (Stocker and Irvine 1983) and Emus (Noble 1975). Liddy (1985) however, has shown that seeds of *Lantana camara* germinate from Silvereye droppings.

It is difficult to determine the reality of these values for wild birds as stress can clearly speed gut passage rate in captive birds. However, given that all birds experienced stress levels in this experiment the differential rate of passage is still valid. The speed of passage can have important consequences for seed dispersal distances. The distance most seeds are dispersed will be equivalent to the distance the bird travels within the 6–28 minutes it takes for seeds to pass through the gut.

Fullness of gut causes a slower rate of passage of seeds. The consequence of this for laboratory estimates of gut passage rate is that true estimates of passage rate should be measured with birds that have eaten. It is likely that the only time a gut is empty is first thing in the morning.

The consequence of slower gut passage rates for plants with vertebrate-dispersed seeds is that there is likely to be an increase in the dispersal distance of those seeds. However, advantages of seed dispersal must be offset against the loss of viability of seeds. The seed coat of *C. quadrifida* seeds is soft and the digestive juices in the gut may penetrate easily causing mortality of these seeds even after a short exposure period.

This study represents an initial investigation into the processes of seed dispersal following seed removal. We have very little understanding of the fate of seeds once the disperser has removed them from the parent plant. Studies that continue to investigate the differential role of dispersers in affecting viability of seeds and the nature of the seed shadow are needed.

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