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INVASIVE PLANT SEED VIABILITY AFTER PROCESSING BY SOME ENDEMIC GALAPAGOS BIRDS

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Resumen. – La viabilidad de las semillas de plantas invasoras después del procesamiento por aves endémicas de Galápagos. – En las Islas Galápagos, Ecuador, investigamos cómo la viabilidad de semillas de plantas invasoras es afectada por el procesamiento y digestión de aves endémicas, en particular Cucuves de Galápagos (*Nesomimus parvulus*), Pinzones Medianos de Tierra (*Geospiza fortis*) y Pinzones Pequeños de Tierra (*G. fuliginosa*). Se llevaron a cabo múltiples ensayos con cinco aves de cada especie en cautiverio. Se alimentó a las aves con frutos de amaranto (*Amaranthus dubius*), maracuyá (*Passiflora edulis*), mora (*Rubus niveus*), guayaba (Psidium guajava), sauco (*Cestrum auriculatum*) y lantana (*Lantana camara*). El Cucuve de Galápagos es probablemente un dispersor eficaz de plantas invasoras, debido a que consumió mas fruta que todas las especies de pinzones en la mayoría de los ensayos, y defecó todas las semillas (excepto las de amaranto) sin afectar su viabilidad. Las semillas fueron retenidas en el tracto digestivo por un promedio de 87 min. Como era esperado, los Pinzones de Tierra se comportaron como depredadores de semillas, triturando las semillas antes de ingerirlas. Sólo una semilla viable de mora fue defecada por un Pinzón de Tierra. Las tres especies fueron observadas movilizando frutos y semillas dentro de las jaulas mientras comían. La dispersión de semillas en distancias cortas podría ocurrir de esta manera.

Abstract. – In the Galapagos Islands, Ecuador, we investigated how the seed viability of important invasive plant species was affected by processing and digestion by endemic birds, namely, Galapagos Mockingbirds (*Nesomimus parvulus*), and Medium (*Geospiza fortis*) and Small (*G. fuliginosa*) ground finches. Multiple feeding trials were carried out on five captive birds of each species. They were fed amaranthus (*Amaranthus dubius)*, passion fruit (*Passiflora edulis)*, blackberry (*Rubus niveus)*, guava (*Psidium guajava)*, sauco (*Cestrum auriculatum)*, and lantana (*Lantana camara)*. The Galapagos Mockingbird is likely to be an effective disperser of invasive plants, as it defecated seeds of all species except amaranthus, without lowering their viability. Seeds were retained in the gut for an average of 87 min. Mockingbirds ate fruit in more of the trials than did the finches. Finches are confirmed as seed predators as they generally crushed seeds before ingesting them. Only one intact viable blackberry seed was defecated by a Small Ground Finch. All three bird species were observed moving fruit (and seeds) around their cages while feeding. Seed dispersal over short distances could happen in this way. *Accepted 11 November 2005.*

Key words: Invasive plants, Galapagos birds, seed dispersal.

INTRODUCTION

The introduction, spread and subsequent invasion of alien species has become a problem worldwide, but is of particular concern on oceanic islands (Dulloo *et al.* 2002; Vitousek *et al.* 1997). In the Galapagos Islands, Ecuador, at least 700 alien plant species are known to have been introduced by people, of which at least 235 have naturalized,

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at least 100 have become established in intact native vegetation, and approximately 40 are recognized as having an impact on native vegetation (CDRS Galapagos Flora Database, March 2005).

One of the principal agents of spread of plants to and within the Galapagos Islands is birds. Sixty percent of the natural plant introductions to the Galapagos islands are attributed to birds, 38% internally and 22% attached externally (Porter 1976). Little is known about which birds spread which alien plant species and with what frequency, but introduced and invasive plants now form a large part of the Galapagos flora, especially on the inhabited islands. It is inevitable that the bird fauna which is still dominated by native and endemic species should play a role in their dispersal. In fact dispersability of plants by birds is a key contributor to the invasiveness of a given alien plant species (Daehler *et al.* 2001, Pheloung *et al.* 1999).

Guerrero (2002) observed that, among Galapagos bird species with fruit forming a part of their diet, many species mostly crush seeds, while others normally swallow fruit or seeds whole. The swallowers included the Galapagos Mockingbird (*Nesomimus parvulus*), the Galapagos Flycatcher (*Myiarchus magnirostris*), the Warbler Finch (*Certhidea olivacea)*, and the introduced Smooth-billed Ani (*Crotophaga ani*). Seed crushing is common amongst the ground finches (*Geospiza* spp.) and fruit pulp is often completely removed and seeds are preferentially eaten (Guerrero 2002). Guerrero (2002) documented internal dispersal of seeds of a few introduced plant species. She found intact seeds of *Rubus niveus*, *Capsicum frutescens* and *Lantana camara* in the stomach of Smooth-billed Anis, *Rubus niveus* in the feces of Galapagos Flycatchers, and *Adenostemma platyphyllum* in the feces of Small Ground Finches. The seeds of *Rubus niveus* and *Capsicum frutescens* from Smooth-billed Anis were shown to be viable, but these data were not sufficient to draw broad conclusions about the effect of digestion by these birds on the viability of seeds, or whether common invasive plants are dispersed by birds in Galapagos.

We experimentally tested seed processing by three Galapagos endemic bird species in order to elucidate their potential effectiveness as dispersers of common invasive alien plants. In particular, we were interested in the viability of seeds after being processed by known seed predators and a seed swallower. Gut processing time for the different combinations of birds and plants was also of interest, as time in the gut may be related to dispersal distances. The plants used in the study are all alien invasive species in Galapagos: passion fruit (*Passiflora edulis)*, blackberry (*Rubus niveus)*, guava (*Psidium guajava)*, sauco (*Cestrum auriculatum)*, lantana (*Lantana camara)*, and amaranthus (*Amaranthus dubius)*. All but the latter are considered to be serious invaders in the Galapagos National Park and the agricultural zones of Santa Cruz, and have brought about significant ecosystem changes (Mauchamp 1997, Tye 2000). Amaranthus on the other hand is a common weed of disturbed areas.

METHODS

*Study species and care of birds***.** We studied fruit and seed processing by the Small Ground Finch (*Geospiza fuliginosa*), the Medium Ground Finch (*G. fortis*) and the Galapagos Mockingbird (*Nesomimus parvulus*) and its affect on seed viability. None of the birds is completely frugivorous, though fruit (Galapagos Mockingbird) and seeds (Ground Finches) probably form the bulk of their diet (Grant & Grant 1980, Grant & Grant 1979). These species were selected because they are widespread, common, and easy to catch and keep in captivity. Six Medium (mean weight 22.4 g) and five Small Ground Finches (mean

TABLE 1. Number of trials for each bird-plant combination (excluding Amaranthus).

	Medium Ground Finch	Small Ground Finch	Galapagos Mockingbird	Total
Lantana	12	9	8	29
Blackberry	17	14	9	40
Sauco	15	11	8	34
Whole Guava	9	8	10	27
Half Guava	10	10	10	30
Whole Passion fruit	9	8	4	21
Half Passion fruit	8	9	9	26
Total	80	69	58	207

weight 17.4 g) and five Galapagos Mockingbirds (mean weight 46.8 g) were captured using mist nets at the Charles Darwin Research Station on Santa Cruz Island in May and June 2003. All captured birds were adults. They were kept in captivity for 7–19 days in individual wood framed cages (50 by 50 cm and 100 cm high) inside a shaded wire aviary. The birds were protected from sun, wind, rain, rats, and ants.

We designed a "standard" diet for the birds to keep them in the best possible condition. At times this diet was interrupted by feeding trials with the fruit of the invasive alien species (see below). They had access to dishes of water enriched with the vitamin mixture AD3E, small stones, and a larger bathing dish at all times. Their standard diet consisted of 2-parts protein, 1-part carbohydrate, and 1-part fruit. This diet included fresh insects, grated cheese, grated hardboiled egg whites, oats, rice, fruit (apple, pear, papaya, banana), and *Alternanthera* flowers, as recommended by G. Jimenez (pers. com). When insects were difficult to obtain, the diet was supplemented with a mixture of ox-heart, minced carrot, bread crumbs, fresh cheese, and sand as recommended by S. Tebbich (pers. com.). This diet was not available during the feeding trials but was available after the morning trials were completed until nightfall. Birds were weighed daily and any that fell below 85% of their weight at capture were immediately released. All birds were released at the end of the trials.

Feeding trials. In the trial periods, the birds were fed only the ripe fruit of introduced species. After fasting all night, one to three trials were conducted each morning between 07:30 and 13:00 h, before the birds were fed the standard diet described above. All 15 birds were subject to trials with passion fruit, blackberry, guava, sauco, and lantana depending on the availability of fruit and birds at the time of the trial (Table 1). If a bird had lost some weight, it was given the standard diet as opposed to subjecting it to the feeding trial, so some birds were not subject to the same number of tests. Amaranthus flower heads were fed only to the finches, in part because they were observed to feed on them in the field. In captivity, amaranthus seeds were not eaten (only the leaves and flowers were eaten), so trials were curtailed after two trials.

All fruit were fed to the birds in small bowls whole, except for guavas and passion fruits which were also cut open in some trials (Table 1). The amount of fruit varied between trials; though within a trial it was similar, there was usually more than the birds could eat in 20 min. We were less interested in the amount of fruit consumed than in the fact that the fruit or seeds were eaten, and if seeds sur-

TABLE 2. The number of entire viable and (non-viable) seeds for each plant species defecated by each bird species. Chi^2 comparisons of seed viability between the control and the Galapagos Mockingbird were done. The asterisk (*) indicates a significant result ($P < 0.05$). Controls are fresh seeds taken from plants.

Bird species	Plant species						
	All fruit species	Amaranthus	Guava	Lantana	Passionfruit	Blackberry	Sauco
Medium Ground Finch	0	0	0	0	0	0	0
Small Ground Finch	1 100%	0	0	0	0	1 100%	0
Galapagos Mockingbird	455 (68) 87%	0	105 (22) 82%	16 (4) 80%	30 (4) 88%	216 (24) 90%	167(13)* 93%
Control	938 (125) 88%	0	179 (33) 84%	112 (36) 76%	197 (10) 95%	186 (16) 92%	202 (2) 99%

vived processing in the gut by the birds. Birds had access to the fruit for 20 min during which time their feeding was observed. Observations were also made of the movement of fruit and seeds around the cage by means other than swallowing and defecation (i.e., regurgitation, removing fruit and/or seeds from the dish while mandibulating and moving them short distances within the cage). After 20 min of undisturbed feeding, the fruit was removed, and paper on the floor of cages was examined for feces every 5–10 min for approximately 2 h. Feces found in the cage at the observation time were collected and the time was noted. Thus, most of the recorded times do not represent the precise time of defecation but rather an interval during which the defecation occurred. If more than one defecation was observed during the interval, an average time between defecations was determined for the interval. These data helped us to approximate the elapsed time between feeding and defecation, and between defecations (the sampling units were individual fecal masses observed during a time interval). We noted if there was any indication that the feces contained the fruit being trialed at that time, e.g., coloration or fragments.

Viability analyses. The number of seeds in each fecal sample was counted under a microscope. Defecated seeds were tested for viability by cutting longitudinally, soaking in water for about 16 h, then soaking in a 0.1% solution of 2,3,5-triphenyl-2H-tetrazolium chloride (TTC) for 4 to 5 h. Viable seeds release hydrogen ions during transpiration and combine with TTC causing the live tissue to stain entirely pink or red (Baskin & Baskin 2001, Stanley & Lill. 2002). In the same way, we also tested viability of approximately 200 seeds per plant species which were used as a control. These were collected from ripe fruit at the same time and place as the fruit used in the feeding trials

Statistics. Multiple Chi squared tests were used to compare observed frequencies of viable and unviable seeds defecated by the Galapagos Mockingbird with the control seeds of each of the plant species. In turn, seeds moved while being processed by the bill were compared with the control. Fisher's Exact test for count data was used to compare the proportions of trials in which the different bird species ate the fruit they were fed (Crawley 2005). The nonparametric Spearman rank

TABLE 3. The number of viable and (non-viable) seeds moved from the feeding bowl to other parts of the cage through mandibulating.

Bird species	Plant species					
	All fruit species	Guava	Lantana	Passionfruit	Blackberry	Sauco
Galapagos Mockingbird	82 (13)	5 (1)	22 (6)	25 (5)	29 (1)	1 (0)
Medium Ground Finch	110 (21)	30 (0)	20 (10)	10 (1)	24 (6)	26 (4)
Small Ground Finch	98 (16)	2 (0)	20 (10)	22 (0)	27 (3)	27 (3)
Total	290 (50)	37 (1)	62 (26)	57 (6)	80 (10)	54 (7)

correlation was used to test the relationship of the proportion of viable seeds defecated in a given time interval and gut retention times for each plant species. Confidence intervals were calculated for the time interval between the end of the feeding trials and defecation of seeds and for the interval between defecations. In the case of time to defecation of seeds, data were bootstrapped (resampled 10,000 times with replacement) to estimate confidence intervals. All analyses were carried out using R (R Development Core Team 2005).

RESULTS

The Galapagos Mockingbird defecated viable seeds of all five of the plant species used in the experiment. Lower viability was observed after sauco seeds passed through the gut of the Galapagos Mockingbird in comparison with the control seeds, $\chi^2 = 8.332$, df = 1, $P = 0.004$ (Table 2). Otherwise overall seed viability of the other plant species was not negatively affected by digestion (but see below for comments about relationship between gut retention time and viability). The finches crushed seeds with their mandibles before ingestion, almost without fail (Table 2) and seed fragments were often seen in fecal clumps. One viable blackberry seed was defecated by the Small Ground Finch, and no intact seeds were defecated by the Medium Ground Finch (Table 2). Many seeds were moved around (carried in the mandibles) the cage by all the birds during the trials (Table 3). However, relative to the number of seeds ingested and defecated by the Galapagos Mockingbird, numbers moved in this way were low. On one occasion, we observed a Galapagos Mockingbird regurgitating a lantana seed.

Seeds of passion fruit and guava showed a significant correlation between proportion of viable seeds and time spent in gut. In the case of passion fruit, this relationship was negative ($r_s = -0.506$, df = 18, $P = 0.03$), and positive for guava ($r_s = 0.382$, df = 36, $P = 0.02$).

The three bird species can be ranked by the proportion of trials in which they ate fruit: Galapagos Mockingbird > Medium Ground Finch > Small Ground Finch. The difference was significant between the Galapagos Mockingbird and the Small Ground Finch as determined with a Fisher's Exact test, $P = 0.009$, with an odds ratio between 1.2 and 6.7 (95% confidence interval). But differences between any other combination of birds was not significant using the same test. Pieces of guava fruits presented whole were eaten in a few trials but no unopened passion fruit were eaten in the trials, probably because of their size and their hard skins. Though we observed the birds pecking holes into unopened guavas, no

birds managed to penetrate the thick skin and reach the seeds during the 20 min in which the fruit was available. Mockingbirds did eat and pass viable seeds when offered cut guavas, so they are capable of dispersing seeds.

The Medium Ground Finch had longer intervals between each defecation than the other two bird species as evidenced by 95% confidence intervals around the mean: Small Ground Finch 15.8 min ± 1.3, n = 388 ; Galapagos Mockingbird 14.8 min ± 1.4, n = 224; and the Medium Ground Finch 22.7 min ± 2.7, n = 898. We did not detect differences between time intervals between defecations after trials with respect to plant species. The Galapagos Mockingbird defecated whole seeds on average 87 ± 8 min (95% confidence intervals) after feeding ceased.

DISCUSSION

The Galapagos Mockingbird is a potentially effective disperser of invasive alien plants. Seed processing by the bird does not negatively impact the viability of seeds of the species studied, with the exception of sauco, but even then viability exceeded 90%. The time interval between defecations was similar for all the bird species at approximately 15–20 min. However, in the case of the Galapagos Mockingbird, seeds generally took more than an hour to pass after feeding which suggests a potential for long distance dispersal and a differential gut retention time for soft parts of the fruit and the seeds. The distance that seeds may be dispersed in that time will depend on the bird's movement patterns. Home ranges for Mockingbirds are known to be less than 1 ha generally (Curry & Grant 1989), so most dispersal is likely to be less than 100 m, though the movement of juveniles and occasional exploratory flights may lead to longer distance movement, and birds are known to move between islands occasionally (D. Wiedenfeld pers. com.).

Seed viability before and after processing by Mockingbirds was high for all plant species, though the extent to which this relates to germination rates is not clear since tetrazolium tests generally overestimate germination and the relationship between the two variables needs to be established experimentally (Baskin & Baskin 2001). It is likely that germination rates are lower than the viability levels we detected. In other studies, blackberry and lantana had germination rates of 85% (Landázuri 2002) and 35%, respectively (Ruiz 1992), in Galapagos, though in the latter case seed germination was only followed during a few months.

Ground finches are known seed predators eating both native and introduced species (Grant 1981, Grant & Grant 1980, Guerrero 2002) but Small Ground Finches were shown to be frequent dispersers of smaller seeded native plants and, on occasion, they dispersed introduced species (Guerrero 2002). Only on one occasion in this study did a Small Ground Finch defecate a viable seed (blackberry). This shows that ground finches might occasionally disperse *Rubus niveus* in the wild. This difference between Small and Medium ground finches may relate to the ability of the larger bird to crush seeds. Even seeds that do not get crushed by the bill may not survive the finch's digestive processes. The Galapagos finches have been shown to have extraordinary digestive abilities, e.g., they can digest 90% of pollen ingested, almost two times higher than any other bird species (Grant 1996). Considering that Medium Ground Finches defecated less frequently than the other species, this may be evidence of different digestion efficiencies between the species of finch (Karasov 1990).

In this study, the proportion of viable seeds was both negatively (passion fruit) and positively (guava) associated with time spent in the digestive tract. We suggest that whether or not the relationship between time in the

digestive tract and viability is negative or positive, the process is basically the same. Digestion obviously cannot increase the number of viable seeds passing through the digestive tract, and we suggest that the positive effect on proportion of passed intact seeds that are viable may be due to enhanced digestion of inviable (e.g., immature or damaged) seeds such that they do not come out intact. The negative relationship is probably due to digestive enzymes killing seeds that are still passed apparently intact, such that proportion viable (with live tissue) decreases. Differences between plant species must be related to the relative ability of seeds and the seed coat to withstand digestion. This could be better investigated by feeding Galapagos Mockingbirds a known number of seeds and tracking the proportion that get passed intact, and their viability.

Fruit and seeds were moved around the cage while mandibulating by all the bird species during the trials. The movement of fruit and seeds during feeding was also noted by Guerrero (2002) as a likely means of short distance dispersal. All of the fruit of the invasive species considered in these trials are known to be eaten in the wild by the birds in this study. Only now is it clear whether they are likely to disperse the plants concerned. In this study, only the Galapagos Mockingbird was conclusively shown to defecate viable seeds of the fruit it eats. Other birds in Galapagos known to swallow fruit could be equally effective dispersers of widespread invasive plants, though this should be confirmed. The introduction of other plant species to Galapagos that are known to be bird dispersed and have fruit with small seeds should not be permitted.

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