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NATIVE AND INTRODUCED BIRDS OF GALAPAGOS AS DISPERSERS OF NATIVE AND INTRODUCED PLANTS

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Resumen. – El rol de las aves nativas e introducidas de Galápagos en la dispersión de plantas nativas e introducidas. – Investigamos la dispersión de semillas por siete especies de aves terrestres de Galápagos, seis de ellas nativas o endémicas (Paloma de Galápagos *Zenaida galapagoensis*, Cuclillo canela *Coccyzus melacoryphus*, Pájaro brujo *Pyrocephalus rubinus nanus*, Papamoscas de Galápagos *Myiarchus magnirostris*, Cucuve de Galápagos *Nesomimus parvulus* y Canario de manglar *Dendroica petechia aureola*), además del ave introducida Garrapatero de pico liso *Crotophaga ani*. La mayor parte de estas especies previamente habían sido consideradas principalmente como depredadoras de semillas o insectívoras. Todas fueron registradas comiendo frutos excepto el Pájaro brujo que parece ser exclusivamente insectívoro. El Papamoscas de Galápagos, el Cucuve de Galápagos y el Canario de manglar presentaron en sus heces semillas viables, mientras que las dos primeras de estas tres especies también las regurgitaron. Una gran proporción de las muestras de heces de estas tres especies presentaron semillas viables; por lo tanto son dispersoras frecuentes, potencialmente a larga distancia. La mayor parte de los estómagos de los Garrapateros también contenían semillas viables. Las semillas intactas más frecuentemente encontradas en muestras de heces fueron de frutos carnosos *Tournefortia* spp., *Miconia robinsoniana*, *Scutia spicata* y la invasora introducida *Rubus niveus*. La dispersión de plantas por estas especies de aves es probablemente más común que la antes asumida de sus modelos alimenticios predominantes: depredación de semillas e insectivoría. Las aves terrestres en Galápagos probablemente juegan un rol importante en la biología poblacional de plantas y en la dinámica de la comunidad vegetal, por medio de la dispersión de semillas ingeridas, entre e intra-isla. El Garrapatero de pico liso, ave invasora, podría modificar la dinámica de dispersión de las plantas nativas así como aumentar la cobertura potencial de la mora invasiva *Rubus niveus*.

Abstract. – We investigated seed dispersal by seven Galapagos land-bird species, six of them native or endemic (Galapagos Dove *Zenaida galapagoensis*, Dark-billed Cuckoo *Coccyzus melacoryphus*, Vermilion Flycatcher *Pyrocephalus rubinus nanus*, Galapagos Flycatcher *Myiarchus magnirostris*, Galapagos Mockingbird *Nesomimus parvulus*, and Yellow Warbler *Dendroica petechia aureola*), plus the introduced Smooth-billed Ani *Crotophaga ani*. Most of these were previously regarded primarily as seed predators or insectivores. All were found to eat fruit except the Vermilion Flycatcher, which appears to be exclusively insectivorous. The Galapagos Flycatcher, Galapagos Mockingbird, and Yellow Warbler defaecated viable seeds, while the flycatcher and mockingbird also regurgitated viable seeds. A large proportion of the feces of these three species contained viable seeds; they are therefore common dispersers, potentially over long distances. Most Smooth-billed Ani stomachs also contained viable seeds. The most frequently encountered intact seeds in feces were of the fleshy-fruited shrubs *Tournefortia* spp., *Miconia robinsoniana*, *Scutia spicata*, and the introduced invasive blackberry *Rubus niveus.* Spread of plants by these birds is probably more common than previously assumed from their predominant feeding patterns of seed predation and insectivory. Land birds in Galapagos probably play an important role in Galapagos plant population and vegetation community dynamics, via intra- and inter-island dispersal of ingested seeds. The invasive ani may be changing the dispersal dynamics of native plants as well as increasing the spread of the invasive *Rubus niveus*. *Accepted 11 April 2011.*

Key words: Native plants, introduced plants, native birds, introduced birds, islands, invasive, seed dispersal, Galapagos, frugivory.

INTRODUCTION

Birds probably constituted the most important transport mechanism for colonization of the Galapagos Islands by vascular plants (Porter 1976, 1983). Birds may continue to play an important role in Galapagos plant evolution by dispersing seed over relatively long distances such as between islands, which may also have conservation implications, if they distribute the seeds of plants that have been introduced to Galapagos by people, thereby contributing to the threat that invasive plants pose to the Galapagos biota (Loope *et al.* 1988). Introduced birds may change the natural patterns of dispersal if they too disperse native or introduced plants.

Studies of seed dispersal by Galapagos animals in general were reviewed by Guerrero & Tye (2009); proven dispersers include Galapagos giant tortoises (*Geochelone* spp.) (Rick & Bowman 1961, Rick 1966), Short-eared Owls (*Asio flammeus*) (Grant *et al.* 1975), and the introduced Black Rat (*Rattus rattus*) (Clark 1978). Some Galapagos plant species have been shown to depend on animals for successful dispersal (Clark & Clark 1981).

However, Galapagos has no specialist frugivorous birds. Until recently, most dietary studies of Galapagos land-birds focused on seeds and fruit as bird food, rather than on the impact of the birds on the plants that they eat, whether as seed predators or dispersers. Most such studies assumed or concluded that most land-bird species were either granivores (i.e., seed predators, including many Darwin's finches Geospizinae and Galapagos Dove *Zenaida galapagoensis*) or insectivores (other Darwin's finches, a cuckoo, flycatchers, mockingbirds, and a warbler), and that they do not disperse seeds by endochory at all, or not frequently. However, this conclusion was largely based on lack of evidence, rather than negative evidence, and we showed that at least eight species of Darwin's finch, formerly regarded as primarily granivorous or insectivorous, are actually substantially frugivorous and may be effective dispersers of the seeds of both native and introduced plants over short or long distances in Galapagos (Guerrero & Tye 2009). Earlier, Grant & Grant (1979) showed that the Galapagos Mockingbird (*Nesomimus parvulus*) eats fruit of the Galapagos native trees and shrubs *Bursera graveolens* (Burseraceae), *Croton scouleri* (Euphorbiaceae), *Lantana peduncularis* (Verbenaceae), and *Cordia lutea* (Boraginaceae), among others, that it regurgitates intact seed of *Cordia*, and that on some islands dispersal of the endemic *Opuntia* (Cactaceae) may depend on mockingbirds. Aviary studies have shown that Galapagos Mockingbird feces contained intact seeds of *Solanum cheesmaniae* (Solanaceae), of which 64% germinated, compared with 2% in a control of uneaten seed (Rick and Bowman 1961; Rick 1966), and that Galapagos Mockingbird passes viable seeds of several introduced plant species (Buddenhagen & Jewell 2006). Further, even relatively infrequent passage of occasional undigested seeds by bird species that do not eat much fruit, or that normally digest the seeds they ingest, may be important for the life cycle of a plant species but overlooked or dismissed as unimportant in studies of bird biology.

Having already shown that many species of Darwin's finch that were formerly disregarded as dispersers actually transport large numbers of viable seeds of many plant species (Guerrero & Tye 2009), we here investigate the importance of a range of other Galapagos land-bird species in dispersing and predating the seeds of Galapagos endemic, native, doubtfully native (*sensu* Tye 2006), and introduced plants. Seven resident bird species were included in the study: Galapagos Dove (endemic), Dark-billed Cuckoo (*Coccyzus melacoryphus*, non-endemic native), Smooth-billed Ani (*Crotophaga ani*, of the few bird species introduced to Galapagos by people, the only one that has become widespread in the islands), Vermilion Flycatcher (*Pyrocephalus rubinus nanus*, endemic subspecies), Galapagos Flycatcher (*Myiarchus magnirostris*, endemic), Galapagos Mockingbird (endemic), and Yellow Warbler (*Dendroica petechia aureola*, endemic subspecies). Of these species, the only one for which any previous information on actual or potential seed dispersal existed was the Galapagos Mockingbird, as discussed above.

STUDY AREAS AND METHODS

The study took place on the south side of Santa Cruz Island, in the centre of the Galapagos archipelago. The vegetation of Galapagos is strongly zoned by altitude (Wiggins & Porter 1971). On the southern slopes of Santa Cruz, the Dry Zone of scrub and dry woodland extends up to c. 150 m a.s.l., where it blends into a Transition Zone of closed forest that reaches up to c. 400 m. Above this is the Humid Zone, which can be subdivided according to vegetative formation, including (in order of increasing altitude) the Scalesia Zone humid forest, the Miconia Zone humid shrubland, and the Fern-Sedge Zone dominated by tall herbaceous species. This natural zonation has been interrupted by the creation of an Agricultural Zone which lies mostly within the Transition and Scalesia Zones. Scientific names of plants follow the database of the flora of Galapagos (www.darwinfoundation.org/datazone/checklists), which with few exceptions (based on recent taxonomic work) follows the nomenclatural database of the Missouri Botanical Garden (www.tropicos.org).

Four study sites were selected, in different vegetation zones and with differing contributions of introduced plant species to total plant cover. The sites were:

Sendero Científico (0°44'25.7"S, 90°18'8.7"W): the "research trail" at the Charles Darwin Research Station in Dry Zone open woodland and scrub, with a variety of trees and shrubs, and few introduced plant species.

Los Gemelos (0°37'26.7"S, 90°23'3.8"W): humid forest in the Scalesia Zone, dominated by *Scalesia pedunculata* (Asteraceae) trees, and with an understorey of shrubs and herbaceous plants.

Media Luna (0°39'43.5"S, 90°19'39.4"W): *Miconia robinsoniana* (Melastomataceae) scrub in the Miconia Zone, where the introduced Guava (*Psidium guajava*, Myrtaceae) is common. The ground layer is characterized by a variety of ferns, grasses, and sedges.

Santa Rosa (0°38'9.9"S, 90°23'51.9"W): part of the agricultural area (formerly upper Transition and lower Scalesia zones), where introduced plants dominate.

The flora of each site was catalogued and full site descriptions with a list of species of plant that bear fruit attractive to birds may be found in Guerrero & Tye (2009).

Field observations and analysis of feces and gut contents were used to determine which bird species ate fruit of which plants, and the fate of the seeds. Observations at Sendero Científico were made during January–December 2000, and observations at the other three sites during April 2000 to March 2001. Opportunistic observations were also made at other sites on Santa Cruz, including collection and analysis of gut contents of birds found dead, mostly road deaths.

Observations of foraging were made twice per month, between 08:00 and 11:00 h or between 13:00 and 15:00 h (Galapagos standard time), along a c. 1000-m transect on a pre-existing trail at each site. All feeding episodes were recorded, irrespective of food type eaten. Observations were made at close range, taking advantage of the fact that most Galapagos birds are unafraid of humans, or with the aid of 10 x 25 binoculars. One "observation" means one interaction between a bird and a food species, observed for up to 300 s (timed by stopwatch) or until the bird left or switched food species (cf. Schluter 1982). If the same individual fed at different food species, these were classed as separate observations. This could conceivably lead to bias due to the preferences of individual birds. However, the 181 foraging observations were collected from almost 300 hours of observation (only 0.6 per h over all species), over a period during which mist-netting indicated large, mobile populations of four species at all sites (unpublished results). Further, occasions when more than one successive observation was made on the same individual made up < 2% of observations. Therefore we consider it unlikely that individual preferences would have significantly biased the results.

Two fruit-seed handling techniques were observed: A) "swallow": the entire fruit, or pieces of it, was swallowed whole, along with intact seeds; B) "crush": the bird destroyed the seed with its bill and ate it. No species was seen to eat only fruit pulp and discard the seeds without ingesting them (a technique that is used by many Darwin's finch species: Guerrero & Tye 2009).

At least once per month at each study site, birds were captured using 12 x 2.5 m mist nets, opened for 4 h per session, and feces that were deposited in nets or cloth holding bags were collected. Birds were kept in bags for at most 20 min, during which time most defaecated. Bags were cleaned between each use. When birds were seen to defecate on other occasions, the feces were also collected when possible. Feces and gut contents were examined under a stereo-microscope, and seeds, fruit fragments, and other food items were counted and identified as far as possible, with the aid of a seed reference collection built up during the study, herbarium specimens, and literature.

Seeds found in fecal and gut samples were washed, then maintained for up to five months on damp tissue paper in open Petri dishes in a light window, to encourage germination and prove viability, as well as permit identification of unidentified seeds. Seeds whose radicle attained at least 1 mm length were considered viable.

RESULTS

During the study, 36 of the 181 feeding observations (20%) were of birds eating fruit or seeds. In total, 340 samples were obtained of feces (314 samples), stomachs (20), and regurgitated pellets (6). Intact seeds were found in samples from all bird species studied (Table 1), except the Vermilion Flycatcher.

Treatment of fruit and seeds by birds. The Smooth-billed Ani, Galapagos Flycatcher, and Galapagos Mockingbird always swallowed fruit (Fig. 1). The Galapagos Dove was only seen to crush seeds (Fig. 1), but its single fecal sample contained two intact seeds among other seed fragments (Table 2), so it must sometimes swallow seeds whole.

No feeding observations of the Dark-billed Cuckoo were obtained but the few stomach samples (Table 2) suggest that it swallows fruit. The few Smooth-billed Ani

TABLE 1. Fecal, stomach, and regurgitated samples with fruit remains, intact and viable seeds. Percentages are of number of samples. [1]All of the samples contained intact seeds.

Species	Total no. of samples	Fecal samples			Stomach samples			Regurgitated samples		
		No.	No. with fruit or seed remains[1]	No. (%) with viable seeds	No.	No. with fruit or seed remains[1]	No. (%) with viable seeds	No.	No. with fruit or seed remains[1]	No. (%) with viable seeds
Galapagos Dove	1	1	1 (100)	0	0	-	-	0	-	-
Dark-billed Cuckoo	4	0	-	-	4	3 (75)	0	0	-	-
Smooth-billed Ani	7	0	-	-	7	6 (86)	3 (50)	0	-	-
Galapagos Flycatcher	103	101	27 (27)	10 (37)	0	-	-	2	2 (100)	1 (100)
Galapagos Mockingbird	41	36	26 (72)	14 (54)	1	1 (100)	1 (100)	4	4 (100)	2 (50)
Yellow Warbler	179	171	11 (6)	5 (46)	8	0	-	0	-	-
TOTAL	340	314	65 (21)	29 (9)	20	10 (50)	4 (40)	6	6 (100)	3 (60)

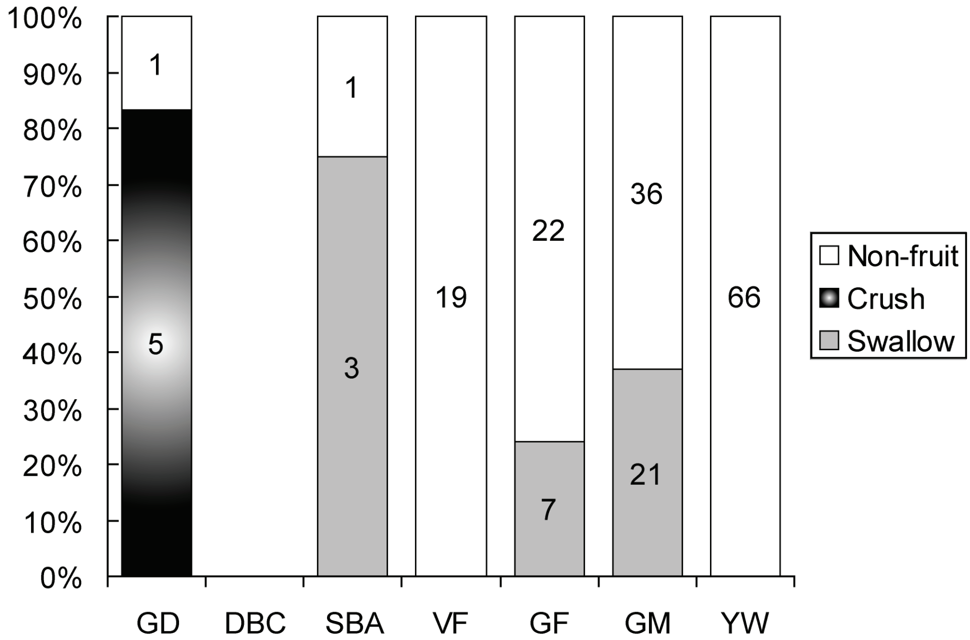

FIG. 1. Frequency (n on bars) and proportion of feeding observations and seed treatments for different bird species. Bird names abbreviated as follows: GD = Galapagos Dove, DBC = Dark-billed Cuckoo, SBA = Smooth-billed Ani, VF = Vermilion Flycatcher, GF = Galapagos Flycatcher, GM = Galapagos Mockingbird, YW = Yellow Warbler.

feeding observations reveal that fleshy fruit are eaten (Table 3), while stomach samples contained seeds of a variety of fleshy-fruited species (Table 2), fruit pulp, and fragments of insects.

The Vermilion Flycatcher was not seen to eat fruit, and fecal samples provided no evidence of frugivory (Fig. 1, Table 2). All observations and feces indicated exclusive insectivory, although sample sizes for this species were small.

The Galapagos Flycatcher ate fleshy fruit (Tables 2, 3). During observations, it always chose fruit that had either previously been attacked by other birds, leaving the pulp exposed through broken skin, or (in the case of *Momordica*) fruit that had opened to reveal the seed plus aril which the bird then swallowed. However, samples indicate that it also swallowed whole intact fruit of some species. One regurgitated pellet contained fragments of insects, a seed of *Scutia spicata* (Rhamnaceae) (5.0 mm maximum dimension, from fruit mean max. diam. 7 mm), and a seed of *Tournefortia psilostachya* (Boraginaceae) (mean max. diam. 2.3 mm, from fruit mean max. diam. 5.7 mm); another pellet contained two *T. psilostachya* seeds. Seeds of *Scutia* were not found in faeces of this species, but *T. psilostachya* seeds were.

The Galapagos Mockingbird ate fruit during 37% of observations, and took a wide variety of fleshy fruit (Tables 2, 3), which were always swallowed. One sample contained immature seeds of *Cardiospermum galapageium* (Sapindaceae), whose fruit is a dry capsule. In this case the unripe capsule or seeds might be the nutritive part selected by

TABLE 2. Number (%) of fecal, stomach, and regurgitated samples from each bird species, which contained intact seeds of different plant species. Bird names abbreviated as follows: GD = Galapagos Dove, DBC = Dark-billed Cuckoo, SBA = Smooth-billed Ani, VF = Vermilion Flycatcher, GF = Galapagos Flycatcher, GM = Galapagos Mockingbird, YW = Yellow Warbler. Fruit types: d = dry fruit, including grass grains, achenes, and dry capsules; f = fleshy fruit, including berries, drupes, arillate seeds, and fleshy capsules.

		Birds (no. of samples)							
Plant species	Fruit type	GD	DBC	SBA	VF	GF	GM	YW	Total
		(1)	(4)	(7)	(5)	(103)	(41)	(179)	(340)
Endemic plants									
Castela galapageia	f	-	-	-	-	-	1 (2)	-	1
Cardiospermum galapageium	d	-	-	-	-	-	1 (2)	-	1
Miconia robinsoniana	f	-	-	-	-	6 (6)	-	5 (3)	11
Scutia spicata	f	-	-	-	-	1 (1)	7 (17)	-	8
Tournefortia pubescens	f	-	-	-	-	1 (1)	11 (27)	-	12
Non-endemic native plants									
Laportea aestuans	d	-	-	-	-	1 (1)	-	-	1
Solanum americanum	f	-	-	2 (29)	-	3 (3)	-	-	5
Tournefortia psilostachya	f	-	2 (50)	4 (57)	-	12 (12)	15 (37)	4 (2)	37
Doubtfully native plants									
Paspalum conjugatum	d	-	-	-	-	1 (1)	-	1 (1)	2
Introduced plants									
Adenostemma platyphyllum	d	-	-	-	-	-	-	1 (1)	1
Capsicum frutescens	f	-	-	1 (14)	-	-	-	-	1
Lantana camara	f	-	-	1 (14)	-	-	-	-	1
Momordica charantia	f	-	-	-	-	-	2 (5)	-	2
Rubus niveus	f	-	-	1 (14)	-	5 (5)	-	-	6
Unidentified plants									
Dry-fruited species	d	1 (100)	-	-	-	-	-	-	1
Unknown fruit type	?	-	1 (25)	1 (14)	-	1 (1)	1 (2)	-	4
Total samples with seeds		1 (100)	3 (75)	6 (86)	0	29 (28)	31 (76)	11 (6)	81 (24)

the bird. Four regurgitated pellets contained seeds of *Castela galapageia* (Simaroubaceae) (5.0 mm, from fruit 9 mm diam.), *Momordica charantia* (Cucurbitaceae) (4.5 mm), and *Scutia spicata*. *Castela* and *Momordica* were only found in mockingbird pellets, while *Scutia* seeds were also found in its feces.

The Yellow Warbler was not observed eating fruit, but seeds of fleshy fruit were found in several samples (Table 2).

A few samples from the Galapagos Flycatcher and Yellow Warbler contained single examples of dry fruit, including grass grains and achenes of *Adenostemma* (Asteraceae) (Table 2).

Treatment of fruit and seeds of different plants. Species whose seeds were commonly swallowed, and therefore potentially dispersed over long distances, included small-seeded, fleshy-fruited species (*Miconia*, *Scutia*, *Solanum*, *Tournefortia*, *Rubus*), and larger-seeded fleshy-fruited species, such as *Castela*, *Cordia*, and *Momordica*. Fruit of some dry-fruited species

TABLE 3. Frequency of observations of feeding on different fruit species, and handling treatments applied to each fruit species (c = crush; s = swallow). Bird names and fruit types abbreviated as in Table 2.

Plant species	Fruit type	Birds			
		GD	SBA	GF	GM
Endemic plants					
Castela galapageia	f	-	-	-	1 (s)
Miconia robinsoniana	f	-	-	1 (s)	-
Scutia spicata	f	-	-	-	5 (s)
Tournefortia pubescens	f	-	1 (s)	-	6 (s)
Non-endemic native plants					
Cordia lutea	f	-	-	-	2 (s)
Panicum dichotomiflorum	d	1 (c)	-	-	-
Solanum americanum	f	-	1 (s)	-	-
Tournefortia psilostachya	f	-	-	-	6 (s)
Doubtfully native plants					
Paspalum conjugatum	d	1 (c)	-	-	-
Portulaca oleracea	d	2 (c)	-	-	-
Introduced plants					
Digitaria horizontalis	d	1 (c)	-	-	-
Momordica charantia	f	-	-	2 (s)	1 (s)
Rubus niveus	f	-	1 (s)	4 (s)	-

(grasses and *Portulaca*) were mostly crushed (Table 3), although fecal samples showed that some of these were swallowed and survived the digestive process.

Of the 81 fecal and stomach samples that contained intact seeds, 74 (91%) had seeds from fleshy fruits, 7 (9%) had seeds of dry-fruited species (*Cardiospermum*, *Laportea*, *Adenostemma*, and grasses), and 3 (4%) had seeds from undetermined fruit type (Table 2). The most frequently encountered intact seeds were *Tournefortia psilostachya* (in 11% of all 340 samples), *Tournefortia pubescens* (Boraginaceae) (4%), *Miconia robinsoniana* (3%), *Scutia spicata* (2%), *Rubus niveus* (Rosaceae) (2%). *Solanum americanum* (Solanaceae), *Momordica charantia*, *Paspalum conjugatum* (Poaceae), and *Adenostemma platyphyllum* (Asteraceae) were each present in 1% of the samples, with *Capsicum frutescens* (Solanaceae), *Castela galapageia*, *Lantana camara* (Verbenaceae), and others in < 1%.

The proportion of seeds that germinated averaged higher in stomach and regurgitated samples than in fecal samples (Table 1), which suggests that the digestive process of the birds destroys some seeds that were swallowed intact. Germination is proof of viability but lack of germination does not necessarily imply that all seeds of the species were killed by the digestive process, since some may have been ingested when immature, or the conditions of the germination experiment may not have favored germination of some species (such as those with a dormancy period greater than five months). All of the seeds that germinated were of fleshy-fruited species (Table 4).

Site differences in seeds eaten and dispersed. Both bird feeding behavior and the fruit species most commonly seen eaten differed at the different study sites, in large part related to different plant availability and bird species abundance at each site (unpubl. data),

TABLE 4. Viability of intact seeds found in fecal, regurgitated, and stomach samples.

Plant species	Feces				Stomachs				Regurgitated pellets			
	No. of samples with seeds	No. with seeds that germinated	No. of seeds	No(%) of seeds that germinated	No. of samples with seeds	No. with seeds that germinated	No. of seeds	No(%) of seeds that germinated	No. of samples with seeds	No. with seeds that germinated	No. of seeds	No(%) of seeds that germinated
Endemic species												
Cardiospermum galapageium	1	0	2	0 (0)	0	-	-	-	0	-	-	-
Castela galapageia	0	-	-	-	0	-	-	-	1	1	1	1 (100)
Miconia robinsoniana	11	9	1017	775 (76)	0	-	-	-	0	-	-	-
Scutia spicata	6	5	7	5 (71)	0	-	-	-	2	2	2	2 (100)
Tournefortia pubescens	11	3	46	9 (20)	0	-	-	-	1	0	2	0 (0)
Native species												
Laportea aestuans	1	0	1	0 (0)	0	-	-	-	0	-	-	-
Solanum americanum	3	2	10	6 (60)	2	1	1345	722 (54)	0	-	-	-
Tournefortia psilostachya	29	10	105	17 (16)	7	1	1178	3 (0.3)	1	0	1	0 (0)
Doubtfully native species												
Paspalum conjugatum	2	0	2	0 (0)	0	-	-	-	0	-	-	-
Introduced species												
Adenostemma platyphyllum	1	0	1	0 (0)	0	-	-	-	0	-	-	-
Capsicum frutescens	0	-	-	-	1	1	65	1 (2)	0	-	-	-
Lantana camara	0	-	-	-	1	0	12	0 (0)	0	-	-	-
Momordica charantia	0	-	-	-					2	0	2	0 (0)
Rubus niveus	5	0	10	0 (0)	1	1	203	52 (26)				
Undentified plants												
Dry-fruited species	2	0	2	0 (0)	1	0	1	0 (0)	0	-	-	-
Unknown fruit type	2	0	2	0 (0)	1	0	2	0 (0)	0	-	-	-
TOTAL	74	29	1205	812 (67)	14	4	2806	778 (28)	7	3	8	3 (38)

suggesting that the bird species concerned were primarily opportunistic rather than selective among fruit species. At Sendero Científico, the fruit of *Tournefortia pubescens*, *T. psilostachya*, and *Scutia spicata* were the most commonly consumed. At Los Gemelos, only two bird species were seen eating fruit: Galapagos Dove, which ate grass grains, and Smooth-billed Ani, which ate *Solanum americanum*. At Media Luna, *Miconia robinsoniana* was the most frequently consumed fruit. At Santa Rosa, the fruit of the introduced *Rubus niveus* was the most commonly eaten species.

DISCUSSION

All of the species studied, except the Vermilion Flycatcher, ate at least some fleshy fruit and swallowed seeds, and are therefore potential seed dispersers.

The Galapagos Flycatcher, Galapagos Mockingbird, and Yellow Warbler all defaecated viable seeds, while the flycatcher and mockingbird also regurgitated viable seeds. These three species are thus proven seed dispersers, which transport seed away from the parent plant. This confirms previous studies of the Galapagos Mockingbird (Rick 1966, Grant & Grant 1979, Rick & Bowman 1981, Buddenhagen & Jewell 2006), but the Galapagos Flycatcher and Yellow Warbler have previously been considered pure insectivores (Harris 1974, Castro & Phillips 1996). Other Neotropical tyrannid flycatchers also consume substantial quantities of fruit which, in the case of island species, may be associated with competitive release and limitation of individual food resources, as in the case of the Cocos Island Flycatcher (*Nesotriccus ridgwayi*), whose ecology is comparable with that of the Galapagos Flycatcher (Sherry 1985, pers. observ.).

The Galapagos Dove is mainly a seed predator but may also be a disperser, as are many granivorous Darwin's finches (Guerrero & Tye 2009). The Dark-billed Cuckoo was not proven to be a disperser in this study although sample sizes were too small to eliminate it as a potential disperser.

Stomachs of the introduced Smooth-billed Ani also contained viable seeds (no fecal samples were obtained of this species). Subsequent studies have shown that the Smooth-billed Ani is an important disperser of the introduced invasive Hill Blackberry (*Rubus niveus*) in Galapagos; indeed it may be considerably more effective in dispersing *Rubus* seeds than any native Galapagos landbird (Soria Carvajal 2006), thus potentially enhancing the plant's invasiveness in the archipelago.

For some fleshy-fruited Galapagos native plants such as the shrubs *Miconia robinsoniana*, *Tournefortia* spp., and *Cordia lutea*, relatively long-distance endochorous dispersal by at least the Galapagos Flycatcher, Galapagos Mockingbird, and Yellow Warbler, and now also by the introduced the Smooth-billed Ani, could be important in their population dynamics, with the ani perhaps having so-far undetermined impacts on the dispersion dynamics of native Galapagos plants. Seeds of these species may be commonly dispersed at least far enough to take them away from the parent plant, whereas occasional long-distance dispersal, even between islands, could result in major range changes, of great importance on an evolutionary time-scale.

These bird species could also conceivably bring about long-distance and inter-island dispersal of invasive species, such as *Rubus niveus*, thereby creating new foci of invasion. Genetic evidence suggests that the strongly-flying Galapagos Dove regularly moves between islands (Santiago-Alarcón *et al.* 2006), as does the Smooth-billed Ani (Soria Carvajal 2006), so they could act as long-distance dispersers of a variety of plant species, including invasives.

The spread of plants by several of the bird species we studied is likely to be greater than previously suspected from their common feeding patterns of seed predation and insectivory, because of this hitherto undetected but important intake of fruit. This study, along with recent evidence from the largest group of Galapagos land-birds, the geospizine finches (Guerrero & Tye 2009), suggests that land-birds in Galapagos play an important role in Galapagos plant population and vegetation community dynamics, via intra- and inter-island dispersal of ingested seeds, and including the occasional colonization of new sites.

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