PREDATION ON SEEDS OF INVASIVE LANTANA CAMARA BY DARWIN’S FINCHES IN THE GALAPAGOS ISLANDS

JORGE CARRIÓN-TACURI,1,4 REGINA BERJANO,1 GIOVANNY GUERRERO,2 ENRIQUE FIGUEROA,1 ALAN TYE,3 AND JESÚS M. CASTILLO1

ABSTRACT.—Observations on birds feeding on fruits of the invasive shrub Lantana camara (Suirrosa) were conducted on Santa Cruz Island, Galapagos (Ecuador) in the Dry Zone during the 2009 dry season. The endemic ground finches Geospiza magnirostris (Large Ground Finch) and G. fortis (Medium Ground Finch) were recorded eating Lantana seeds with G. fortis the main consumer (> 90% of records). Both finch species crushed the seeds and ate the embryos, discarding the exocarp and empty seed coats. They also dropped entire fruits to the ground, which could contribute to short-distance dispersal, but both finches also consumed fruits of L. camara on the ground. Density of L. camara seedlings under adult plants was higher in rockier areas than in bare soil since seeds were less accessible to predators and/or found more suitable microsites for germination and establishment. Both species of finches serve as short-distance dispersers, but mainly as seed predators of L. camara fruits. Received 8 July 2011. Accepted 15 November 2011.

The introduction, spread, and subsequent invasion of alien species has become a problem worldwide, but is of particular concern on oceanic islands (Vitousek et al. 1997, Dulloo et al. 2002, Kueffer et al. 2010). The geographic isolation of islands limits immigration of new species while those that arrive subsequently evolve with fewer competitors and predators. The accelerated introduction of new species by people alters the natural ecological equilibrium of islands and can exert severe pressure on native species biodiversity (MacArthur and Wilson 1967).

Frugivorous animals, by acting as seed vectors, have an essential role in the reproductive cycle of their food plants (Herrera 1995). Disperser availability may be an important factor affecting invasion success, and alien plants arriving in new habitats have no guarantee of finding suitable dispersal agents (Parker 2001). However, Richardson et al. (2000) noted that invasive plants rarely suffer from a lack of mutualistic services such as pollination and fruit dispersal. Birds are recognized as the main dispersal agent of many invasive plant species around the world (e.g., Dean and Milton 2000, Renne et al. 2002, Gosper et al. 2005), and may directly affect conservation efforts.

Entire seeds passed through the gut of frugivore birds often have increased germination rates, although they may also lose viability and reduce germination (Traveset 1998, Orrock 2005, D’Avila et al. 2010). Seed predators may also contribute to dispersal if pulp is consumed and seeds are discarded in suitable microsites (Shiels 2011). However, when seeds are crushed before ingestion, their viability is reduced as recently demonstrated for frugivores and seed predators in the Galapagos Islands (Buddenhagen and Jewell 2006, Guerrero and Ty 2009, Guerrero and Ty 2011).

Lantana camara (Verbenaceae) (Suirrosa) is one of the most invasive plants in the Tropics, now occupying a wide variety of habitats in >60 countries worldwide (Parsons and Cuthbertson 2001). It was introduced to the Galapagos Islands as an ornamental species in 1938 (Tye 2001) and, in 1987, covered >2,000 ha (Lawesson and Ortiz 1990). L. camara produces a great number of fruits (Sharma et al. 2005) that are usually dispersed by frugivorous birds (Day et al. 2003). However, no specialist frugivores occur in the Galapagos Islands and most landbird species of the archipelago were traditionally considered to be granivores (seed predators) or insectivores (Guerrero and Ty 2009). However, some birds, including Darwin’s finches, may act as dispersers for short and long distances of endemic, native, and introduced plants (Buddenhagen and Jewell 2006; Guerrero and Ty 2009, 2011; Heleno et al. 2011). Guerrero and Ty (2009, 2011), report Darwin’s finches and other Galapagos birds demonstrate three main types of fruit-seed handling techniques: (1) swallow the entire fruit or pieces of it, (2) discard the seeds, eating only the pulp, and (3) crushing the fruit and seed. Our objectives were to: (1) analyze the interaction of Galapagos bird species with L. camara fruits.
during the dry season in the dry lowlands of Santa Cruz Island, and (2) investigate seed dispersal, seed predation, and seedling colonization pattern.

METHODS

Study Site.—The Galapagos Islands are ~960 km west of Ecuador in the Pacific Ocean. The vegetation of Galapagos is strongly zoned by altitude and aspect with the Dry Zone being most extensive, occupying the majority of the lowlands of the archipelago (McMullen 1999, Trueman and d’Ozouville 2010). Two distinct seasons can be distinguished during the year in the Galapagos (Trueman and d’Ozouville 2010). The warm season (January to June) is caused by warm ocean currents sweeping southward from Central America. Mean daily maximum temperature is 29 °C and mean daily temperature is between 25 and 26 °C (Ziegler 1995). During this season, the skies are normally clear, but heavy showers are frequent; this season is the wettest in the Dry Zone of the archipelago (Trueman and d’Ozouville 2010). Two distinct seasons can be distinguished during the year in the Galapagos (Trueman and d’Ozouville 2010). The warm season (January to June) is caused by warm ocean currents sweeping southward from Central America. Mean daily maximum temperature is 29 °C and mean daily temperature is between 25 and 26 °C (Ziegler 1995). During this season, the skies are normally clear, but heavy showers are frequent; this season is the wettest in the Dry Zone of the islands. The cool season (July to December) is caused by the Humboldt Current, resulting in cooler air temperatures (18–26 °C) with skies usually overcast. A mist layer, known locally as ‘garúa’, frequently occurs at higher elevations, but little precipitation occurs in lowlands (Ziegler 1995); this season is the driest in the lowlands (Trueman and d’Ozouville 2010).

Our study was conducted in the dry lowlands at 26 m above sea level on Santa Cruz Island (90 19' W, 00 44' S) near Puerto Ayora. The vegetation at the study site was dominated by the native tree Bursera graveolens (Burseraceae) (51% relative cover) and the endemic Galapagos lantana Lantana peduncularis (Lantana peduncularis) (46% relative cover). The relative cover of L. camara was 37% (relative cover was measured by contact every 50 cm along five linear transects, each of 30 m).

Study Species.—L. camara is a pantropical species inhabiting a wide variety of habitats around the world (Sharma et al. 2005). It usually colonizes open sunny areas such as degraded lands, grasslands, crops edges, abandoned crop fields, and coastal areas or forest edges. It also colonizes forests after disturbances including fire or logging (Parsons and Cuthbertson 2001). Fruits of L. camara are two-seeded drupes, 4–8 mm in diameter, green and hard when immature, turning to shiny purple/black when ripe (Auld and Medd 1987, Parsons and Cuthbertson 2001).

Sampling.—Our study was conducted during August and September 2009, when L. camara was finishing fruiting and fruit pulp was dry. Bird activity was observed from sunrise to midday, as preliminary sampling confirmed that most foraging activity was concentrated in this period. We conducted 24 hrs of observations on five different mornings recording bird species and foraging behavior at five individual shrubs of L. camara. Information on foraging behavior for each bird included: number of infructescences visited, fruits consumed per foraging bout, and bird behavior after feeding. Birds were identified following Swash and Still (2000).

Fruit productivity of L. camara in our study site was measured for 10 tagged adult plants. The total number of infructescences per plant and the total number of fruits per infructescence (10 infructescences/plant) were recorded. The area occupied by each plant was recorded to calculate fruit production/m².

Ten other adult plants of the same population were tagged to record fruit removal. Twenty infructescences of these plants were carefully bagged with fine mesh nylon for 1 month to measure fruit fall without external intervention. Fruit traps consisting of plastic containers 28 cm in diameter and 8 cm deep covered with 1-cm metallic wire mesh were placed under the marked plants to collect fallen fruits. The mesh prevented further predation once the fruit entered the container. Ten additional plots (10 × 10 cm) were marked on the ground surface near the tagged L. camara plants and 25 L. camara fruits were placed in each. These were followed during 1 month to measure predation of fruits on the ground.

Colonization patterns of L. camara seedlings were studied by recording their presence under 10 adult plants. The percentage of soil covered by rocks was also recorded under each adult Lantana plant to investigate the effect of substrate at colonized sites, especially the effect of rocky habitats in seedling establishment.

Statistical Analysis.—Analyses were conducted using SPSS Release 18.0 (SPSS Inc., Chicago, IL, USA). Deviations were calculated as the standard error of the mean (SEM). Outlier values were identified and discarded following the formula (mean ± 2 SD’s). Pearson correlation coefficient was used to assess correlation between the behavior of birds after feeding on L. camara and the number of eaten fruits, and between the number of seedlings and the percentage of soil covered by rock.
TABLE 1. Number of recorded visits per bird species, visited infructescences (mean ± SE), consumed fruits per bout, and per infructescence in the Dry Zone of Santa Cruz (Galapagos Islands) during the 2009 cool–dry season.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. visits (%)</th>
<th>Visited infructescences per bout</th>
<th>Consumed fruits per infructescence</th>
<th>Consumed fruits per bout</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geospiza fortis</td>
<td>83(92)</td>
<td>6 ± 1</td>
<td>5 ± 0</td>
<td>26 ± 4</td>
</tr>
<tr>
<td>G. magnirostris</td>
<td>7(8)</td>
<td>22 ± 9</td>
<td>3 ± 1</td>
<td>60 ± 22</td>
</tr>
</tbody>
</table>

RESULTS

*L. camara* plants produced an average (± SE) of 1,075 ± 158 infructescences, each containing 12 ± 1 fruits per infructescence. Adult *L. camara* plants had an area of ~6.0 ± 0.8 m², and were 2.5 ± 0.2 m in height on average; thus, each plant produced a mean of 2,820 ± 229 fruits/m². Only four (2%) of a total of 252 fruits in the bagged infructescences fell into the bags after 1 month.

Ninety records of birds feeding on *L. camara* fruits were obtained during 24 hrs of observation: 8% corresponded to the Large Ground Finch (*Geospiza magnirostris*) and 92% to the Medium Ground Finch (*G. fortis*) (Table 1). Neither finch species swallowed entire fruits of *L. camara*, but crushed them, eating the embryo and endosperm and discarding the empty fruit coat. *G. fortis* removed 2,138 fruits and *G. magnirostris* 149 fruits. *G. magnirostris* ate fruits from an average of 22 ± 9 infructescences on each visit to a *L. camara* plant, consuming 3 ± 1 fruits per infructescence. *G. fortis* visited 6 ± 1 infructescences, consuming 5 ± 0 fruits per infructescence (Table 1). The number of fruits removed per foraging bout was variable: 1–157 fruits for *G. magnirostris* and 1–207 fruits for *G. fortis*. On average, *G. magnirostris* ate 60 ± 22 fruits per bout and *G. fortis* 26 ± 4 fruits per bout (Table 1). Some fruits were observed falling intact to the ground as a consequence of infructescence manipulation by both species of finches.

Most *G. fortis* (59%), after feeding on *L. camara,* flew from the area (out of sight), while 25% flew to a nearby tree, 12% continued feeding on another *L. camara* plant, and 4% flew to the ground and continued foraging. Twenty-nine percent of the *G. magnirostris* flew from the area after feeding on *L. camara,* 29% flew to a nearby tree, 29% continued eating on another *L. camara* plant, and 13% flew to the ground (Fig. 1). The behavior of finches after feeding on *L. camara* was independent of the number of fruits eaten (Pearson correlation coefficient, *P* > 0.05).

Fruit traps under *L. camara* plants collected an average of 684 ± 105 fruits/m² during a month, which represented 24% of the fruit production of a plant (Fig. 2). Of the trapped fruit, 311 ± 59 were entire fruits and 373 ± 67 were empty fruit coats, indicating seed predation on the plant. Thus, 13% of the fruit production was consumed on the plant, while 11% was dislodged, mostly as a consequence of infructescence manipulation (Fig. 2).

After 1 month, 66% of the fruits placed in plots on the ground had been removed by unknown agents, 15% were crushed and eaten in situ (fruit remains were found, similar to those dropped by finches), and 19% remained intact on the soil surface (Fig. 2).

The number of seedlings under adult *L. camara* plants varied from 0 to 12, resulting in an average of 1 ± 0 seedlings/m². A significant positive correlation was found between seedling density and percentage of soil covered by rock (*r* = 0.67, *P* < 0.05, *n* = 9), discarding as outlier an adult plant under which there was a high density of seedlings (3 seedlings/m²) and 50% rock cover.

DISCUSSION

Our results demonstrate that seeds of invasive *L. camara* are part of the diet of endemic ground finches (*G. magnirostris* and *G. fortis*) during the cool-dry season in the Dry Zone of Santa Cruz Island (Galapagos). Guerrero and Tye (2009) and Buddenhagen and Jewell (2006), reported ground finches most commonly crush dry seeds. We also found that both finch species behaved mostly as seed predators of *L. camara* rather than dispersers, crushing the dry fruits and feeding on seed embryos.

Ground finches, despite their predominantly predatory role in this study, may also act as short-distance dispersers as their foraging activities caused fruit drop, which may be important given the low percentage of fruit drop from bagged infructescences. *G. magnirostris* visited many infructescences and ate many fruits per bout, but this species was only occasionally observed. *G. fortis* visited more plants, ate at fewer infructescences per plant and ate less fruits per bout, but...
ate more fruits per infructescence. *G. fortis* thus moved less on each *L. camara* shrub and would probably stimulate less fruit fall. Thus, *G. fortis* may be a more effective seed predator and perhaps a less effective short-distance disperser of *L. camara*, as it ate a larger proportion and dislodged a smaller proportion of the fruit than were removed from the bush by its activity at each visit.

Both species of finches also foraged on the ground, which reduces their role as short distance dispersers. Fifteen percent of the fallen fruits appeared to have been removed by the two finch species from the ground during just 1 month.

A great number of fruits on the ground were removed, many of them probably by introduced rodents. This may be effectively equivalent to predation since rodents either eat seeds or store them in deep larder hoards from which successful seedling establishment is unlikely (Montgomery and Gurnell 1985, Hulme 1998). Reducing dispersal distances acts to concentrate seeds...
around parent plants, making them especially vulnerable to seed predators (McConkey and Drake 2002, Chimera and Drake 2011), in this case, ground finches or rodents. However, introduced rodents act as both seed predators and seed dispersers, which may also contribute to the spread of *L. camara* as occurred in the Hawaiian Islands (Shiels 2011, Shiels and Drake 2011). Most seedlings recorded under *L. camara* adult plants were rooted in fissures between rocks where they were less accessible to predators. Seeds of *L. camara* would have a higher probability to survive post-dispersal predation in fissures between rocks, and/or they would find more appropriate environment for germination and establishment as soil moisture is higher than on non rocky surfaces.

Introduction of invasive species can alter ecosystem function, resulting in direct species replacement and changes in ecosystem processes that control plant and animal activities (Mack and D’Antonio 1996). Food during the cool dry season in the Dry Zone of Galapagos is scarcer than during the wetter season, and availability of *L. camara* fruits represents an important food source for the finches. Availability of the invasive *Lantana* could be altering the feeding behavior of endemic finches, and changing their interactions with endemic or native plant species such as *L. peduncularis*, which also grows in the Dry Zone invaded by *L. camara*. It is not known whether the availability of the more abundant *L. camara* fruits might benefit the endemic congener by reducing predation pressure by finches, or whether it might disadvantage it, by reducing dispersal of its fruit. Little predation was observed on *L. peduncularis* fruits (just 6% of the total fruit production, unpubl. data).

Transport of seeds by frugivores from the parent plant could improve the overall chances of seedling dispersal to suitable establishment sites (Schupp 1993, 1995; Schupp and Fuentes 1995) but no birds were observed carrying *L. camara* fruits. Our observations were concentrated in the dry season, when fruits are completely dry and perhaps relatively unappetizing for frugivores, although at higher altitudes it was observed that both finch species also crushed fresh fruits of *L. camara* (J. Carrión-Tacuri, pers. obs.). Further study in the warm wet season in the lowlands, when fruits are mature but still fresh, is needed to evaluate the real dispersal potential.

Intact seeds of *L. camara* have been found in the stomach of the invasive Smooth-billed Ani (*Crotophaga ani*) (Guerrero and Tye 2011). Thus, an introduced bird species could be a long distance disperser of *L. camara* fruits in Galapagos, as in the Hawaiian Islands, where no native bird has been observed eating *L. camara* fruits but six introduced bird species have been implicated in its spread (Perkins and Swezey 1924, Day et al. 2003, Chimera and Drake 2010). Experiments with captive Galapagos Mockingbirds (*Mimus parvulus*) revealed they eat *L. camara* seeds, and seed viability was not significantly different after passing through its gut (Buddenhagen and Jewell 2006).

Effective vertebrate seed dispersal is an important attribute of successful woody plant invaders (Rejmánek 1996, Westcott and Fletcher 2011). *L. camara* already occupied 2,000 ha in the Galapagos Islands by 1987, and the absence of specialist frugivores in the islands may reduce the dispersal and invasion velocity of *L. camara*. Seed predation by the endemic ground finches and other animals may reduce *L. camara*’s rate of spread and therefore its impact on the Galapagos ecosystem (finches removed ~15% of *L. camara* fruits in just 1 month). This effect could be reduced by birds such as the Smooth-billed Ani, which was introduced to Galapagos in 1960s (Rosenberg et al. 1990), or other generalist frugivores that could facilitate seed dissemination and invasion of *L. camara* or other fleshy-fruited non-native species.

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LITERATURE CITED


