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SHORT COMMUNICATION

Galápagos land iguana (*Conolophus subcristatus*) as a seed disperser

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Abstract

The role of the most common land iguana (*Conolophus subcristatus*) in the Galápagos Islands as an effective seed disperser is explored in this study. A total of 5705 seeds of 32 plant species were identified from 160 scats, 4545 of which (80%) appeared visually undamaged. Germination trials of 849 seeds from 29 species revealed that at least 10 species remained viable after passing through the iguana's gut, although only a small proportion of those seeds (4%) germinated. In any case, we argue that *C. subcristatus* exerts an important role on the 7 Galapagos islands where it occurs because of its abundance and capacity to ingest and disperse seeds at long distances. Our results strongly suggest that the Galápagos *C. subcristatus* plays an important role as a seed disperser of not only of native species but also some introduced plants in the Galápagos Islands.

Key words: *Conolophus subcristatus*, Fernandina Island, Galápagos Islands Saurochory, seed dispersal

INTRODUCTION

Seed dispersal and pollination are 2 key services provided by animals to plants. On oceanic islands, where strong isolation limits the arrival of medium and large sized mammals (Gorman 1979), tortoises, iguanas or lizards often undertake an important ecological role as seed dispersers (Olesen & Valido 2003). Furthermore, the reported niche expansion or interaction release of island vertebrates, which tend to occupy underexplored ecological niches and adopt super-generalized diets, magnifies the ecological importance of insular native fauna (MacArthur *et al*. 1972; Cox & Ricklefs 1977; Traveset *et al*. 2015).

The capacity to disperse seeds is largely limited by animal body size and, consequently, by their gape width. Therefore, large animals are disproportionately important as seed dispersers in most ecosystems (Blake *et al.*

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2012; Galetti *et al*. 2015). For instance, the Galápagos giant tortoise is the largest terrestrial animal in the archipelago and was found to be pivotal for vegetation dynamics by dispersing the seeds of many plants over long distances (Heleno *et al.* 2011; Blake *et al*. 2012). The second largest terrestrial animals in the Galápagos are the endemic land iguanas (*Conolophus* spp.), represented by 3 endemic species currently distributed in 7 islands (Fernandina, Isabela, Santa Cruz, Santa Fé, Plazas, Baltra and Seymour) (Jiménez-Uzcátegui *et al*. 2014). However, except for a few anedoctal records (reviewed in Heleno *et al*. 2011), the dispersal potential of the Galápagos land iguanas has never been explored. The 3 Galápagos land iguanas are vegetarian and highly generalized (Jackson 1994): for example, consuming fruits of *Opuntia* spp., *Psidium galapageium* and *Scutia spicata* (Carpenter 1969; McMullen 1999). They feed mostly on low-growing vegetation as iguanas do not climb/creep, although they can stand on their hind legs. It is known that in Fernandina, female iguanas migrate long distances (approximately 10 km) and ascend up to 1500 m, from the sea shore to the central crater of this volcanic island where they lay their eggs (Werner 1983). The population of *Conolophus subcristatus* (Gray, 1831) reaches high densities in Fernandina, with thousands of reproductive females (Werner 1983).

To disclose the potential role of Galápagos land iguanas as seed dispersers, we looked for intact seeds in the scats of *C. subcristatus* of the island of Fernandina and interpreted legitimate seed dispersal based on seed germinability tests.

MATERIAL AND METHODS

Fernandina is the youngest (0.3 Myr, Ali & Aitchison 2014) and westernmost Galápagos island, consisting of a single active shield volcano (last eruption in 2009), with a 5-km wide crater. The island is 642 km^2 and the maximum elevation is approximately 1500-m a.s.l. It is very heterogeneous in ecological conditions, bearing habitats rich in resources for iguanas as well as much bare soil that is used for their burrow construction (Werner 1983). The vegetation patterns are largely determined by volcanic activity and deposition, and the slopes of the volcano are mostly barren lava (Hendrix & Smith 1986). In the lowlands, most vegetation is found in small crevices within the recent lava fields. There is low water availability in this zone, and the black lava can reach over 60 °C on sunny days during the hot season (Christian *et al*. 1983). Information on plant richness in this arid zone can be found in Jaramillo *et al.* (2014). Iguanas are usually concentrated in areas with vegetation (Werner 1983). The predominant plant species in our study area were, in order of abundance: *Bursera graveolens*, *Lantana peduncularis* Andersson, *Boerhaavia caribaea Darwiniothamnus lancifolius* Hook. f., *Cordia leucophlyctis Waltheria ovata* Cav., *Scutia spicata* and *Cryptocarpus pyriformis* Fernandina has never had human settlement despite its large size, and partially for this reason is one of the world's most pristine tropical islands and harbors very few introduced species (Jaramillo *et al*. 2014), none of them vertebrates. Moreover, the population of land iguana of Fernandina is the only one in Galápagos that remain mostly undisturbed, as all other populations have been under anthropogenic stressors such as direct disturbance and the introduction of feral dogs, pigs, goats, cats and rats (Snell *et al*. 1984).

In February 2010 and 2011, we collected scats of *C. subcristatus* in the remote Cabo Douglas (northwest of Fernandina). The scats were collected in an area of approximately 1 km^2 of the arid zone, which holds most plant diversity and endemic species and is the most abundant habitat type in the Galápagos (Guézou *et al.* 2010). This area was scanned by 5 observers and all iguana scats, either fresh or old, were collected as long as they kept their intact structure. This allowed us to study its diet over a relatively long period of time, given that scats remain intact for many months (pers. observ.) mainly due to the large quantity of plant fiber ingested and to the dry climate. Our direct observations of iguanas in the study area lead us to think that the scats might belong to a few dozens individuals. All collected scats were taken to the Charles Darwin Foundation's laboratory in Santa Cruz, where seeds were extracted and identified by comparison with a reference collection of seeds from the archipelago. All seeds were counted and visually inspected under a stereomicroscope and classified as either damaged or undamaged.

As a second step, to evaluate the capacity of seed germination, we carried out an experiment by sowing 849 seeds from 29 plant species found in the scats. Seeds, previously extracted from the surrounding fecal material, were sown on 1 April 2011, on trays of 104 units previously filled with a substrate composed of agricultural soil, volcanic lapilli and turf (2:1:1 ratio). In a shaded greenhouse, soil in trays was kept moist throughout the experiment. Seedling emergence was recorded for 2 years: every other day during the first year and once a week during the second year. In addition, we performed a seed viability analysis, by applying the bioindicator 2,3,5 triphenyl-2H-tetrazolium chloride diluted to 0.1% for 24 h in the dark and at room temperature (Porter *et al.* 1947; Marrero *et al.* 2007) to 4 of the fleshy-fruited plant species found in the scats and, when possible, comparing estimated viability with that of fruits collected directly from wild plants (control treatment).

RESULTS

Of the 160 scats of *C. subcristatus* collected, 148 scats (93%) contained at least one undamaged seed. A total of 5705 seeds of 32 plant species were identified, 4545 of which (80%) appeared visually undamaged, although the proportion of damaged seeds varied considerably across species (mean = 17%, SD = 24.5%, minimum = 0%, maximum = 80%; Table 1). In the scats, seeds were always embedded within fibers and other plant material. Two thirds (63%) of the plant species whose seeds were found in the scats were native, of which a third (31%) were endemic to the Galápagos. Two species (6%) were likely introduced (*Ipomoea* cf. *nil* and *Bidens pilosa*), and the remaining 31% could not be identified and, thus, were scored as of unknown origin. The vast majority (approximately 82%) of the identified plant species produced dry fruits while the rest were fleshy-fruited species (Table 1, Fig. 1). Seeds of the endemic *Scalesia affinis*, *Jasminocereus thouarsii* and *Euphorbia punctulata* (Table 1) were present in higher proportions in the scats (high frequency of occurrence -FO). The FO of each species in the scats ranged from 0.6% (*Bursera graveolens*) to 56.3% (*S. affinis*, Table 1).

Overall, 8 species (Fig. 1) accounted for a large fraction (86.6%) of all intact seeds in the iguana scats; 2 of these were the fleshy-fruited endemics *J. thouarsii* and *L. peduncularis* and the remaining species had dry fruits: *Exodeconus miersii*, *S. affinis*, *E. punctulata*, *Portulaca* sp., *Spermacoce* cf. *remota*, and an unidentified species.

Germination trials showed that of the 849 sown seeds, only a small proportion (4%) germinated. Some of the species (*J. thourasii*, *Portulaca* sp., *Commicarpus tuberosus* and *Boerhavia coccinea*) took >200 days to germinate, whereas others such as *S. affinis* germinated only a few weeks after sowing (Table 1). The viability tests of fleshy-fruited species showed that the seeds of *Castela galapageia* were as viable as those from control plants (G-test: G = 0.38, df= 1, P = 0.53; Table 2), whereas the seeds of *L. peduncularis* showed very low viability. None of the seeds of *B. graveolens* and *S. spicata* recovered from the scats were viable; however, it was not possible to estimate the effect of ingestion on seed viability for these species as we could not evaluate the viability of control (uningested) seeds.

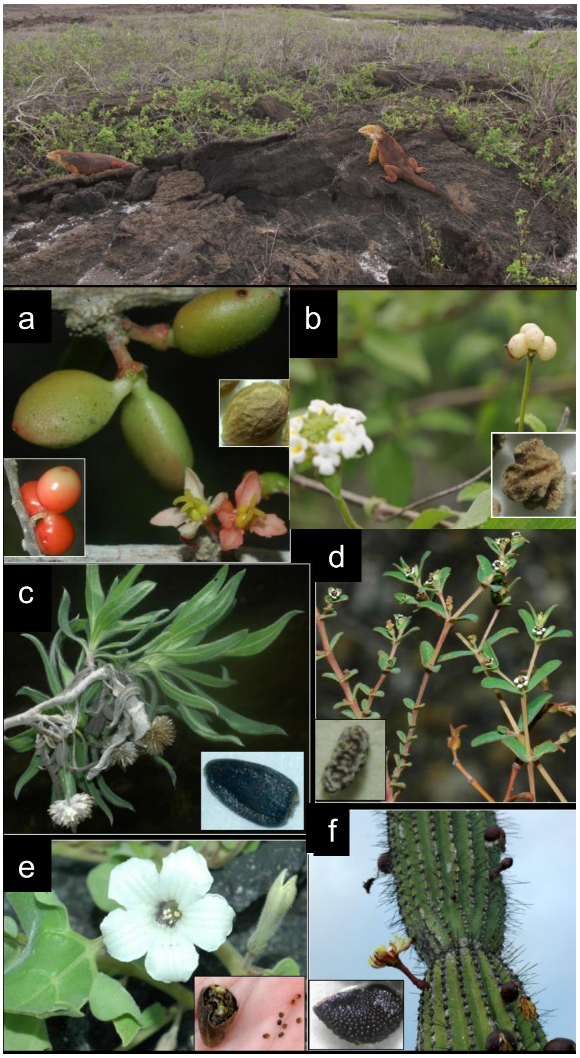

Figure 1 *Conolophus subcristatus* individuals in Fernandina Island (top image) and some of the most frequent plants, whose seeds were found in their scats: (a) *Castela galapageia*, (b) *Lantana peduncularis,* (c) *Scalesia affinis*, (d) *Euphorbia punctulata,* (e) *Exodeconus miersii* and (f) *Jasminocereus thouarsii*. Seeds of each species are shown as insets (also fruits in a).

Table 1 Frequency of occurrence of viable and damaged seeds retrieved from 160 scats of *Conolophus subcristatus* in the island of Fernandina in 2010 and 2011. Germination rate for each seed species and mean number of days to germination are included. Plant origin indicated as: (End) Endemic, (QEnd) Questionably Endemic, (Nat) Native, (Int) Introduced, (QInt) Questionably introduced, (?) Unknown.

Species (origin)	Family	Fruit type	2010	2011	Frequency of occurrence: n. scats w/ seeds	% scats w/ seeds	n. scats w/ intact seed	% scats w/ intact seeds	Number of seeds: n. all seeds	% all seeds	intact	% damaged seeds	n. seeds sown	Germination: n. seeds germinated	% germination	Mean days to germination
Exodeconus miersii (End)	Solanaceae	Dry		X	4	2.5	4	2.5	1185	20.8	1185	0	52	3	5.8	139
Scalesia affinis (End)	Asteraceae	Dry	X	X	89	56.3	78	49.4	985	17.3	772	22	104	14	13.5	16
Jasminocereus thouarsii (End)	Cactaceae	Fleshy	X	X	38	24.1	38	24.1	724	12.7	724	0	104	5	4.8	266
Euphorbia cf. *punctulata* (End)	Euphorbiaceae	Dry	X	X	48	30.4	41	25.9	758	13.3	554	27	104	0	0.0	
Portulaca sp. (?)	Portulacaceae	Dry	X	X	9	5.7	9	5.7	296	5.2	290	2	52	3	5.8	241
unknown seed 1 (?)	/	/	X	X	14	8.9	8	5.1	747	13.1	185	75	42	2	4.8	320
Lantana peduncularis (End)	Verbenaceae	Fleshy	X	X	15	9.5	15	9.5	113	2.0	113	0	52	0	0.0	
Spermacoce cf. *remota* (Nat)	Rubiaceae	Dry	X	X	10	6.3	10	6.3	112	2.0	110	2	32	0	0.0	
unknown seed 2 (?)	/	/	X		2	1.3	2	1.3	81	1.4	81	0	0	/	/	
Stylosanthes sympodiales (Nat)	Fabaceae	Dry	X	X	12	7.6	10	6.3	76	1.3	76	0	0	/	/	
Bidens pilosa (QInt)	Asteraceae	Dry	X	X	14	8.9	9	5.7	130	2.3	75	42	0	/	/	
Convulvulaceae sp.1 (?)	Convulvulaceae	Dry	X		6	3.8	6	3.8	75	1.3	75	0	32	0	0.0	
Poaceae sp.1 (?)	Poaceae	/	X	X	8	5.1	8	5.1	70	1.2	67	4	35	1	2.9	19
Boerhavia coccinea (Nat)	Nyctaginaceae	Dry	X	X	36	22.8	23	14.6	74	1.3	45	39	36	2	5.6	332
Castela galapageia (End)	Simaroubaceae	Fleshy	X	X	16	10.1	16	10.1	35	0.6	35	0	27	3	11.1	28
Oxalis sp.1 (?)	Oxalidaceae	Dry	X		4	2.5	4	2.5	36	0.6	26	28	26	0	0.0	
Ipomoea cf. *nil* (Int)	Convolvulaceae	Dry		X	3	1.9	3	1.9	35	0.6	24	31	24	2	8.3	103
Scutia spicata (QEnd)	Rhamnaceae	Fleshy	X	X	11	7.0	7	4.4	70	1.2	20	71	24	0	0.0	
Bursera graveolens (Nat)	Burseraceae	Fleshy	X		1	0.6	1	0.6	19	0.3	19	0	12	0	0.0	
unknown seed 3 (?)	/	/	X	X	9	5.7	6	3.8	24	0.4	15	38	14	1	7.1	19
Tephrosia cinerea (Nat)	Fabaceae	Dry	X	X	9	5.7	9	5.7	18	0.3	15	17	10	0	0.0	
Ipomoea incarnata (Nat)	Convolvulaceae	Dry		X	3	1.9	2	1.3	14	0.2	12	14	12	0	0.0	
Blainvillea dichotoma (Nat)	Asteraceae	Dry	X		1	0.6	1	0.6	4	0.1	4	0	4	0	0.0	
Varronia leucophlyctis (End)	Boraginaceae	Fleshy		X	3	1.9	3	1.9	4	0.1	4	0	4	0	0.0	
unknown seed 4 (?)	/	/	X	X	1	0.6	1	0.6	4	0.1	4	0	4	0	0.0	
Setaria setosa (Nat)	Poaceae	Dry		X	2	1.3	2	1.3	3	0.1	3	0	3	0	0.0	
Cyperus cf. *anderssonii* (End)	Cyperaceae	Dry	X		2	1.3	2	1.3	2	0.0	2	0	34	0	0.0	
Rhynchosia minima (Nat)	Fabaceae	Dry	X	X	2	1.3	2	1.3	2	0.0	2	0	2	0	0.0	
Poaceae sp.2 (?)	Poaceae	Dry		X	4	2.5	1	0.6	5	0.1	1	80	1	0	0.0	
Brachiaria multiculma (End)	Poaceae	Dry	X	X	2	1.3	1	0.6	2	0.0	1	50	1	0	0.0	
unknown seed 5 (?)	/	/	X	X	1	0.6	1	0.6	1	0.0	1	0	1	0	0.0	
Sida cf. *salviifolia* (Nat)	Malvaceae	Dry	X		1	0.6	1	0.6	1	0.0	1	0	1	0	0.0	
					n=160 scats				5705	100	4541		849	36		

Table 2 Seed viability (identified by the staining of active tissues with tetrazolium chloride) of four fleshy-fruited species found in the scats of *Conolophus subcristatus* in the island of Fernandina. Control seeds are directly collected from plants in the study area.

Plant species	% viability (no. viable seeds/no. tested seeds)	
	Control seeds	Dispersed seeds
Bursera graveolens	0 (0/18)	0 (0/7)
Castela galapageia	60 (18/48)	56 (5/9)
Lantana peduncularis	/	4 (1/24)
Scutia spicata	/	0 (0/7)

DISCUSSION

Our study shows that the Galápagos *C. subcristatus*, acts as a legitimate seed disperser of at least 10 plant species in the lowlands of Fernandina, as their seeds passed intact through the iguana's guts. Moreover, these species, were frequently found in iguanas' droppings, suggesting that this land iguana is a common disperser of such plants. A previous study had already suggested that *C. subcristatus* aids in seed dispersal of some species and that it is most important for revegetation after volcanic activity (Hendrix & Smith 1986). Specifically, these authors found abundant seeds of *Solanum erianthum* in iguana droppings, of which approximately 10% germinated. They claimed that iguanas might be implicated in the distribution of this plant species into areas devoid of vegetation around the main volcanic crater. Our study confirms the role of the Galápagos land iguana as a seed disperser and expands its likely contribution to the dispersal of many plants in the dry lowland areas.

This land iguana includes both fleshy and dry fruits in its diet, as found in other studies on *C. subcristatus* in the mainland (e.g. Traveset 1990; van Marken Lichtenbelt 1993; Blázquez & Rodríguez-Estrella 2007; Moura *et al*. 2015) or in continental islands (Govender *et al*. 2012; Burgos-Rodríguez 2014). Fleshy fruits, together with leaves, are probably a good source of water for these animals in arid environments, and in particular in the dry season. Some studies in the mainland have also reported land iguanas as effective dispersers of seeds in sites that are suitable for germination and establishment (e.g. Benítez-Malvido *et al*. 2003).

Most seeds in the iguana scats were from native plants, either endemic or not. Nevertheless, we also detected seeds of likely introduced plant species, namely *Bidens pilosa* and *Ipomoea* cf. *nil*, as well as seeds from a genus comprising introduced species (e.g. *Portulaca* sp.). The seeds of the alien *Ipomoea* cf. *nil*, for instance, were able to germinate after being ingested by the iguana, which suggests that this disperser might facilitate the invasion of introduced species in Fernandina. Our report represents one more example of native dispersers integrating alien plants in the seed dispersal interactions networks (see Traveset & Richardson [2014] and references therein). Other native dispersers in Galápagos, such as birds, tortoises and lava lizards, have also been shown to contribute to the dispersal of alien plants across the islands (Heleno *et al*. 2013), a phenomenon that is of major concern in the archipelago (Guézou *et al*. 2010).

Many seeds escaped destruction in the iguana's gut and were defecated intact, as has also been reported for other land iguana species, such as the green iguana (*Iguana iguana*) (e.g. Moura *et al*. 2015). Moreover, a variable fraction of the defecated seeds were viable and capable of germinating. Some studies have even reported an increase in the seed germination rate after passing through iguanas' guts, attributing this to their long gut-passage times, often more than 5 days (Benítez-Malvido *et al*. 2003; Morales-Mávil *et al*. 2007). In any case, overall germination of the seeds found in the scats (some of which had been potentially deposited several months ago at the time of collection) was rather low.

However, considering the local abundance of land iguanas, and the large amount of seeds ingested by these animals, even if only a small proportion germinates, they can be considered important for plant dissemination to new areas on this young island. Keystone plant species in the community, such as *L. peduncularis*, *J. thouarsi* or *S. affinis*, may to a large extent benefit from the dispersal by this land iguana. Seed dispersal studies in Galápagos have received considerable attention, with approximately 50 studies having reported the dispersal of at least 178 plant species by 42 disperser species (see Guerrero & Tye 2011; Heleno *et al*. 2011 and references therein; Blake *et al*. 2012; Heleno *et al.* 2013; and Heleno *et al*. unpublished data, including the screening of over 4000 animal droppings collected by our team over 5 years across 12 Galápagos islands). Although sampling in Galápagos across sites and seasons is still scarce, it is remarkable that entire seeds of at least 4 species found in this study, *J. thouarsii*, *S. affinis*, *Stylosanthes sympodiales* and *Tephrosia cinerea*, all native, have not been found yet to be dispersed by any other animal (Table 1). These data, together with the still relatively small effort dedicated to evaluate seed dispersal by land iguanas, clearly show the potential role of this species as a seed disperser in the archipelago and highlight the need for further research on the topic.

The species-poor plant community of Fernandina, mostly formed by scattered *Bursera* trees, *Castela* and *Lantana* shrubs and *Jaminocereus* cacti, is served by a scarce community of seed dispersers, namely mockingbirds (*Mimus parvulus*) and some finch species (Thraupidae), land iguanas (*C. subcristatus*) and lava lizards (*Microlophus albemarlensis*) (pers. observ.). In this pristine and simplified community, the land iguanas might well exert an important role because of their abundance and capacity to ingest and disperse seeds at long distances, as inferred by their long gut-retention times; that is, they might be acting as a keystone species. Nonetheless, iguanas might also have an important antagonistic effect, at least on some of the species, by consuming their leaves and flowers. Therefore, in those cases, the positive effect of the iguana on the plants could be counteracted by its negative effect. Whether such effects are overall positive or negative for each plant species would be worth examining in future studies. Our results strongly suggest that the Galápagos *C. subcristatus* plays an important, and mostly underappreciated, role as a seed disperser in Fernandina, and that the role of this and other species of land iguanas in the archipelago deserves further attention.

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