

# 1 Non-Native Small Terrestrial Vertebrates in the Galapagos

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## 14 **Introduction**

15 Movement of propagules of a species from its current range to a new area—i.e., extra-range  
16 dispersal—is a natural process that has been fundamental to the development of biogeographic  
17 patterns throughout Earth's history (Wilson et al. 2009). Individuals moving to new areas usually  
18 confront a different set of biotic and abiotic variables, and most dispersed individuals do not  
19 survive. However, if they are capable of surviving and adapting to the new conditions, they may  
20 establish self-sufficient populations, colonise the new areas, and even spread into nearby  
21 locations (Mack et al. 2000). In doing so, they will produce ecological transformations in the  
22 new areas, which may lead to changes in other species' populations and communities, speciation  
23 and the formation of new ecosystems (Wilson et al. 2009).  
24

25 Human extra-range dispersals since the Pleistocene have produced important distribution  
26 changes across species of all taxonomic groups. Along our prehistory and history, we have aided  
27 other species' extra-range dispersals either by deliberate translocations or by ecological  
28 facilitation due to habitat changes or modification of ecological relationships (Boivin et al.  
29 2016). Over the last few centuries, human globalisation has led to the integration of most areas of  
30 the planet. Due to transportation advancements, humans and our shipments travel faster and  
31 further than ever before. Unintentionally or deliberately, thousands of species of flora, fauna and  
32 microorganisms have been translocated to places they would never have reached on their own  
33 and beyond the biogeographic barriers that typically prevented their spread in such a timeframe  
34 (Ricciardi 2007). However, most translocated species are already adapted to anthropogenic  
35 niches (especially the ones that are unintentionally introduced), and since their new arrival areas  
36 are usually also under anthropogenic impact, their adaptation process and possibility of survival  
37 are increased.  
38

39 Non-native species contribute to Earth's biota homogenization, but ongoing scientific debates on  
40 the processes, effects, importance and management of non-native species are intense (Davis  
41 2003; Brown and Sax 2004, 2005; Cassey et al. 2005; Dukes and Mooney 2004; Davis et al.  
42 2011; Chew and Carroll 2011; Ricciardi et al. 2013; Simberloff et al. 2013; Chew 2015;

43 Kuebbing and Simberloff 2015; Pereyra 2016; Sol 2016). Non-native species may modify  
44 biological communities and ecosystem functions by becoming, for example, predators,  
45 competitors, preys, seed dispersers, parasites, disease vectors, or ecosystem engineers (Daszak et  
46 al. 2000; Crooks 2002; O'Dowd et al. 2003; Doody et al. 2009; Capps and Flecker 2013;  
47 Ricciardi et al. 2013; Simberloff et al. 2013). Non-native species may have economic, social,  
48 cultural and health impacts on human populations (Vitousek et al. 1997; Pejchar and Mooney  
49 2009). Non-native species that are successful and spread in their new areas become invasive, and  
50 have been described as major anthropogenic drivers of current changes in biodiversity (Vitousek  
51 et al. 1997; Chapin III et al. 2000; Mace et al. 2005; Clavero and García-Berthou 2005; Bellard  
52 et al. 2016; Doherty et al. 2016). Yet, evidence, scientific perspectives and practical implications  
53 for this assertion are still under examination (Gurevitch and Padilla 2004a,b; Ricciardi 2004;  
54 Didham et al. 2005; MacDougall and Turkington 2005; Young and Larson 2011; Russell and  
55 Blackburn 2017).

56  
57 In spatially restricted ecosystems, such as island and wetlands, the effects of invasive non-native  
58 species on native biodiversity can be severe and lead to extensive transformation of native  
59 ecosystems and even the extinction of endemic species (Davis 2003; O'Dowd et al. 2003;  
60 Blackburn et al. 2004; Mace et al. 2005; Simberloff et al. 2013). The Galapagos Islands are a  
61 region of particular interest and relevance to the issue of species introduction and invasiveness.  
62 In the most recent comprehensive review on the Galapagos non-native vertebrates, Phillips et al.  
63 (2012a) pointed out that vertebrate introductions in Galapagos are shifting away from  
64 intentionally introduced species, such as domestic mammals, towards hitchhiking species, such  
65 as reptiles (Phillips et al. 2012a). Furthermore, the authors remarked that snakes and lizards—  
66 i.e., squamate reptiles—could pose the greatest threat the Galapagos' biodiversity in the future.  
67 Like an unfortunate prediction, while Phillips and collaborators were writing their article, the  
68 Common House Gecko *Hemidactylus frenatus*, a lizard profiled as highly invasive, had already  
69 arrived in Galapagos (Torres-Carvajal and Tapia 2011). Despite the fact that only five years have  
70 passed since Phillips et al. (2012a), the panorama of non-native terrestrial vertebrates in  
71 Galapagos has changed in important ways, in particular for non-mammals. Although Phillips et  
72 al. (2012a) and previous studies have dealt with the impacts and management of non-native  
73 species in Galapagos, most studies have focused on domestic species gone feral. Very little  
74 information is available on wild non-native species that have been unintentionally introduced.  
75 Thus, in this publication I analyse the current status of all non-native amphibians, reptiles and  
76 birds that have been reported in the Galapagos Islands, provide new evidence about their  
77 relationship with native and non-native species, comment on their invasiveness and impact  
78 potential, and propose that it is important to rethink about how we understand, manage and  
79 prevent introductions of non-native species. The new wave of introduced species in Galapagos is  
80 formed by small hitchhiker species that are easily overlooked, may travel in high numbers, and  
81 are highly linked to human-made environments.

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### 83 **The Galapagos Islands: An overview**

84 The volcanic marine islands of the Galapagos archipelago are separated from the nearest  
85 mainland—the coast of Ecuador—by ca. 930 km. Nineteen main islands (> 1 km<sup>2</sup>) and over 100  
86 islets and rocks constitute the archipelago, totalling ca. 7850 km<sup>2</sup> of land, spread out over ca. 430  
87 km (straight line between the outermost islands: Darwin and Española). The largest islands are  
88 Isabela (4588 km<sup>2</sup>), Santa Cruz (986 km<sup>2</sup>), Fernandina (642 km<sup>2</sup>), Santiago (585 km<sup>2</sup>), San  
89 Cristobal (558 km<sup>2</sup>), Floreana (173 km<sup>2</sup>) and Marchena (130 km<sup>2</sup>) (Snell et al. 1996).

90

91 The Galapagos are among the few Pacific islands that were not settled by aboriginal humans  
92 (Anderson et al. 2016). They were discovered by Fray Tomas de Berlanga in 1535. While pirate  
93 and whaling ships frequently visited the archipelago since the 16th century, the first settlement  
94 was only established in 1832. Nowadays, Santa Cruz, San Cristobal, Isabela and Floreana have  
95 human populations established on the lowlands and highlands. The main cities in each island are:  
96 Puerto Ayora (Santa Cruz), Puerto Baquerizo Moreno (San Cristobal), Puerto Villamil (Isabela)  
97 and Puerto Velasco Ibarra (Floreana). There are airports in Baltra, San Cristobal and Isabela  
98 islands, with connections to Guayaquil and Tababela (Quito) airports in mainland Ecuador. All  
99 populated islands have maritime ports for passengers and freight, with connections to several  
100 international and national ports, including the Ecuadorian ports of Guayaquil, Manta and Salinas  
101 (Cruz Martínez et al. 2007).

102

103 The climate of Galapagos largely depends on the oceanic currents and winds, resulting in  
104 vegetation distribution being determined by orogenic rainfall (Jackson 1993; Wiggins and Porter  
105 1971). On the lowlands, all islands and islets are arid and warm. A narrow belt along coastal  
106 areas, called Littoral Zone<sup>1</sup>, is dominated by salt-tolerant shrubs and small trees. Xerophytic low  
107 scrub, arborescent and shrubby cacti, and thorn woodland and deciduous forest are the main  
108 vegetation on lowlands, i.e., Dry Zone<sup>1</sup>. A Transition Zone<sup>1</sup>, with taller trees, denser canopy and  
109 more mesic conditions than the Dry Zone, appears as elevation rises (plants here are a mix from  
110 lower and higher zones). Moist conditions exist in the higher islands above 300–600 m, where  
111 three vegetation zones have been recognised: Humid Zone<sup>1</sup>, with incremented humidity and  
112 denser vegetation dominated by evergreen species, in particular the endemic Giant Daisy Tree  
113 genus *Scalesia*; Very Humid Zone, with very dense vegetation dominated by the endemic  
114 Galapagos Miconia *Miconia robinsoniana*; and Pampa Zone, treeless and dominated by sedges  
115 and ferns above regional treeline. An Upper Dry Zone<sup>1</sup>—a climatic inversion zone with drier  
116 conditions—exists on the Cerro Azul and Wolf volcanoes, which reach beyond 1000 m above  
117 the main cloud layer. This zone is covered by scrub vegetation dominated by *Opuntia* cacti or  
118 *Scalesia*. On the leeward side of islands, the Littoral, Dry and Transition zones rise higher and  
119 the moister zones may be absent (Wiggins and Porter 1971). The moist zones (Humid, Very  
120 Humid, and Pampa) are only present on the largest islands (i.e., Santa Cruz, San Cristobal, Pinta,  
121 Santiago, Floreana, Isabela, Fernandina). In addition to these natural vegetation zones, humans

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<sup>1</sup> The ecological classification of vegetation is based on the proposal by Wiggins and Porter (1971).

122 have modified large sections of the Dry, Transition, Humid and Very Humid zones on the four  
123 inhabited islands, transforming them into agro-urban areas, where a large amount of non-native  
124 plant species dominate (Wiggins and Porter 1971; Guézou et al. 2010). The Pampa zone has  
125 been enlarged by human activities and grazing by non-native mammals.

126  
127 World-famous for their biodiversity and role in the formulation of the theory of evolution by  
128 natural selection, the Galapagos Islands are home to a vast array of endemic species of flora and  
129 fauna. Galapagos biodiversity evolved in isolation from its continental counterparts. Moreover,  
130 its uniqueness is not just due to differences between insular and continental species, but also due  
131 to a large level of inter-insular endemism. There are many taxa restricted to just one or few  
132 islands (Parent and Crespi 2006; Sequeira et al. 2008; Benavides et al. 2009; Hoeck et al. 2010;  
133 Poulakakis et al. 2012; Torres-Carvajal et al. 2014; MacLeod et al. 2015; Carmi et al. 2016). The  
134 Galapagos archipelago is home to no less than 211 terrestrial vertebrates, including: 6 endemic  
135 species of snakes of the genus *Pseudalsophis*, 24 endemic lizards (genus *Phyllodactylus*,  
136 *Amblyrhynchus*, *Conolophus*, *Microlophus*), 12 endemic giant tortoises of the genus *Chelonoidis*,  
137 160 species of birds (of which 46 taxa are endemic), and 9 species of mammals (of which 7 taxa  
138 are endemic).

139  
140 Human population in Galapagos has increased significantly over the last decades, and  
141 transportation links carrying local travellers, tourists and supplies have facilitated the arrival of  
142 non-native species (Mauchamp 1997; Causton et al. 2006; Tye 2006; González et al. 2008;  
143 Phillips et al. 2012a). Invasive non-native species have been identified as the principal threat to  
144 biodiversity in the Galapagos terrestrial ecosystems (Causton et al. 2006). For example, feral  
145 populations of Dogs *Canis familiaris*, Cats *Felis catus*, Pigs *Sus scrofa* and Black Rats *Rattus*  
146 *rattus* have been reported to predate upon several endemic species, causing serious declines on  
147 the populations of Galapagos Tortoises *Chelonoidis* spp., Galapagos Land Iguanas *Conolophus*  
148 *subcristatus*, Marine Iguanas *Amblyrhynchus cristatus* and Galapagos Penguins *Spheniscus*  
149 *mendiculus*, among others (Konecny 1987; Phillips et al. 2012a). Grazing and trampling by feral  
150 Goat *Capra hircus* have depleted the populations of several native and endemic plants, including  
151 the critically endangered Santiago Scalesia *Scalesia atractyloides* and Floreana Flax *Linum*  
152 *cratericola*, which are now at the verge of extinction (Schofield 1989; Aldaz et al. 1997;  
153 Simbana and Tye 2009). Feral Cattle *Bos taurus* aided the spread of the invasive non-native  
154 Common Guava *Psidium guajava* and other non-native plants by habitat engineering and seed  
155 dispersion (Phillips et al. 2012a). The parasitic fly *Philornis downsi* is causing significant excess  
156 mortality in the endemic and threatened Darwin's Medium Tree Finch *Camarhynchus puper*  
157 (O'Connor et al. 2010). Cottony-Cushion Scale *Icerya purchasi* has become a pest causing  
158 population declines in the endemic Thin-leafed Darwin's Shrub *Darwiniothamnus tenuifolius*  
159 (Calderón-Álvarez et al. 2012). Ambitious programs to control and eradicate non-native species  
160 have been established in the archipelago (e.g., Barnett 1986; Campbell et al. 2004; Cruz et al.  
161 2005; Carrión et al. 2007).

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However, ecological interactions are of a complex nature and non-native species may in some cases contribute to maintaining ecosystem functions in ecosystems experiencing environmental change (Buckley and Catford 2016). For example, Black Rats have become a seed disperser of the endemic *Miconia robinsoniana* in some agricultural areas of San Cristobal Island (Riofrío-Lazo and Páez-Rosas 2015). Black Rats have also become the most important prey for the Galapagos Hawk *Buteo galapagoensis* since the eradication of feral Goats on Santiago Island (Jaramillo et al. 2016). Non-native species may also help managing invasive species, acting as biological controls. The Vedalia Beetle *Rodolia cardinalis* was deliberately introduced in Galapagos to control the spread of *Icerya purchasi* (Calderón-Álvarez et al. 2012).

174 **Definitions**

175 The dichotomy of native/non-native species is a predominant concept in ecology, biogeography  
176 and conservation biology (Mace et al. 2005; Lomolino et al. 2010; Simberloff et al. 2013). It has  
177 been widely adopted in analysis of the conservation of Ecuadorian biodiversity, and particularly  
178 in relation to Galapagos (Josse 2001; Causton et al. 2006). However, a dichotomous approach is  
179 evidently simplistic and even artificial in any complex and dynamic system. The cornerstone  
180 term “native species” is part of an ongoing scientific and philosophical debate about its  
181 conceptual and operational definitions as well as its relevance and applicability in ecological,  
182 conservation, management, sociocultural and economic scopes (Chew and Hamilton 2011,  
183 Clavero 2014, Van Der Wal et al. 2015). A dichotomous approach is hard to make fully  
184 operational, especially in regions where it is difficult to assess the status of an  
185 archaeophyte/archaeozoan versus a native taxon, or where the distinction between native and  
186 non-native taxa is not absolute (Preston et al. 2004). However, these issues are greatly controlled  
187 in Galapagos due to the isolation of the archipelago and the specific date of human arrival.  
188 Although recognising issues associated with a dichotomous approach, I—for the sake of  
189 operational straightforwardness and due to the particular nature of Galapagos geography and  
190 history—use the following working definitions (modified from Pyšek et al. 2009):

191  
192 **Native taxa:** Those that are originated in a given area, or that arrived from an area in which they  
193 are native by their own means. Their successful arrival is due to their adaptation for dispersal and  
194 survival in the physiological and ecological conditions across the dispersal routes, which are not  
195 acting as strict dispersal barriers. Complete or partial synonyms include terms like indigenous or  
196 autochthonous taxa.

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198 **Non-native taxa:** Those that have arrived from an area in which they are non-native, or that  
199 arrived from their native range by extrinsic dispersal mechanisms (i.e., outside of their own  
200 natural dispersal potential). These extrinsic mechanisms provide specific conditions that allow  
201 these taxa to disperse across environments that otherwise would be severe natural barriers in the  
202 same timeframe. Complete or partial synonyms include terms like alien, exotic, non-indigenous  
203 or allochthonous taxa.

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205 To establish working definitions on the basis of ecological and biogeographic criteria only,  
206 human intervention was intentionally left out. While human extra-range dispersals do facilitate  
207 the arrival of non-native taxa via direct or indirect extrinsic mechanisms, natural colonisations  
208 and human-mediated introductions and establishments of non-native species are nevertheless  
209 similar ecological processes (Buckley and Catford 2016; Hoffmann and Courchamp 2016).  
210 Several authors have argued that geographical origin of species should not be used as the only  
211 criteria guiding management/control decisions (Buckley and Catford 2016; Hoffmann and  
212 Courchamp 2016). However, a distinction between natural colonisations and human-mediated  
213 introductions is at least partially necessary when management and control issues are involved.

214 For example, if a species reached a new area by its own means and without the intervention  
215 extrinsic dispersal mechanisms (incl. without human intervention), it would most probably be  
216 able to do so repeatedly as it is evidenced that the species has the capability to disperse across  
217 natural barriers that separated its geographical origin and new areas. Any proposed regulations to  
218 control its population would be insufficient and inefficient as new arrivals would most certainly  
219 keep occurring. On the other hand, a non-native species that solely depends on human-mediated  
220 extrinsic dispersal mechanisms, could be controlled by regulating the aforesaid mechanisms.

221  
222 Therefore, all species that were established in the archipelago before 1535 are considered native.  
223 Species that have apparently reached the archipelago through their own means after 1535 and  
224 that have established populations because of their own successful oceanic dispersal capacities  
225 (and probably with several dispersal events) are also considered native. Due to the long distance  
226 between Galapagos and mainland (or even other islands), all non-native species in the Galapagos  
227 Islands seem to have arrived due to intentional or unintentional mediation of humans.

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### 231 **Non-native amphibians, reptiles and birds**

232 I report herein a total of 25 non-native amphibians, reptiles and bird species in the Galapagos  
233 Archipelago. The changes, when compared to Jiménez-Uzcátegui et al. (2007) and Phillips et al.  
234 (2012a), are in part explainable by a better understanding of some species' status (see species  
235 accounts below for details), but also due to the arrival of new non-native vertebrates (I include  
236 two species not reported in previous reviews). These non-native species are equivalent to 12% of  
237 all Galapagos native amphibians, reptiles and birds. Santa Cruz and San Cristobal are the islands  
238 with the largest amount of reported non-native amphibians, reptiles and bird species (18 spp.  
239 each). Twelve species are reported in Isabela Island, three in Baltra Island and two species in  
240 Marchena and Floreana. The islands of Genovesa, Pinta, Pinzon, and Santiago each have only  
241 one reported species (Table 1).

242  
243 In any environment, there is an introduction-invasion continuum between the arrival of a non-  
244 native species, its establishment and its shift into invasive (Mack et al. 2000; Blackburn et al.  
245 2011; Pereyra 2016). Non-native species introduced to Galapagos are heterogeneous in terms of  
246 their establishment, spread, dominance and impact. Only a fraction of the non-native species that  
247 arrives becomes established, and an even smaller portion is able to have spreading populations—  
248 i.e., become invasive. For example, out of 754 non-native vascular plants recorded by Guézou et  
249 al. (2010) in the inhabited areas of Galapagos, 35% have established populations; and Tye et al.  
250 (2002) classified 5% of those species as invasive. As for insects, 463 non-native species were  
251 reported by Causton et al. (2006) in Galapagos, with at least 73% of them having established  
252 populations and 13% species classified as invasive.

253  
254 In order to provide a straightforward evaluation of the degree of establishment of non-native  
255 amphibians, reptiles and birds in Galapagos—independent of their conservation effects—I adopt  
256 the categories proposed by McGeoch and Latombe (2016), with some modifications (Table 3).  
257 This typology is based on three main aspects: degree of expansion, population size and time  
258 since arrival (McGeoch and Latombe 2016). Since all non-native species were introduced to  
259 Galapagos within the last two centuries, all could be classified herein as recent. However, I  
260 differentiate between historic (the last centuries) and recent (the last decades) translocations.  
261 Also, I take into account the fact that introductions have not been synchronised, and that some  
262 non-native populations are the result of more than one introduction event.

263  
264 Information about establishment, spread, dominance and impacts of non-native amphibians,  
265 reptiles and birds in Galapagos biodiversity is still incomplete. Eleven non-native amphibians,  
266 reptiles and bird species reported in Galapagos did not become established (Table 1). Six species  
267 are established but only as domestic stock. *Columba livia*, a non-native species that was  
268 introduced as domestic and became established, was eradicated. *Gallus gallus* is the only species  
269 currently present in Galapagos with domestic and feral (or semi-feral) populations. Some feral  
270 chickens may have self-sufficient populations, but evidence is unclear. *Hemidactylus frenatus* is

271 newly established, and self-sufficient populations are apparently small, but this species has a  
272 high potential not just to become more broadly established but to spread successfully, and  
273 therefore become invasive. Monitoring is urgently needed to understand the distribution,  
274 populations and impacts of *H. frenatus*. There is evidence that one non-native amphibian, three  
275 non-native reptiles and one non-native bird are established in Galapagos, having self-sufficient  
276 populations (Table 1). However, they do not have the same level of establishment. *Gonatodes*  
277 *caudiscutatus* is classified as constrained, by having large populations but only on a very limited  
278 geographic range, apparently unable to establish new populations despite being in Galapagos for  
279 ca. 200 years. *Scinax quinquefasciatus* is considered as incipient, by having established large  
280 populations but only on a limited geographic range, yet it was introduced recently (ca. 40 years).  
281 *Phyllodactylus reissii* is dispersing, with a large population in Santa Cruz established ca. 40  
282 years ago, and a probably newly established population in Isabela. Finally, *Lepidodactylus*  
283 *lugubris* and *Crotophaga ani* are classified as successful by having large populations established  
284 on many islands. Since *L. lugubris*, *P. reissii* and *C. ani* have self-sufficient and spreading  
285 populations, they are further classified as invasive species.

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### 287 **Non-native amphibians in Galapagos**

288 Amphibians have never been able to establish by their own means in Galapagos. Absence of  
289 native amphibians in Galapagos is not surprising, as most true oceanic islands are devoid of  
290 native amphibians (Zug 2013). Generally, amphibians are poor dispersers across oceanic barriers  
291 due to their high sensitivity to osmotic stress caused by salt water at all ontogenic levels  
292 (Balinski 1981; Duellman and Trueb 1986; Bernabò et al. 2013). However, a number of frog  
293 species have physiological adaptations to tolerate salinity (Balinski 1981; Beebee 1985; Gomez-  
294 Mestre and Tejedo 2003) and oceans are not always strict barriers to the dispersal of amphibians  
295 (Hedges et al. 1992; Vences et al. 2003, 2004; Measey et al. 2007). The oceanic islands of  
296 Mayote, São Tomé and Príncipe have native frogs that seemingly reached the islands by rafting  
297 through ca. 400 km from Africa (Vences et al. 2003; Measey et al. 2007; Bell et al. 2015). The  
298 Seychelles Islands are extraordinary: despite the extreme distance of ca. 1000 km from  
299 Madagascar and ca. 1300 km from Africa, they have one endemic frog species (Maddock et al.  
300 2014). Nevertheless, and contrary to the Galapagos Islands, all oceanic islands with native frogs  
301 generally have humid terrestrial ecosystems almost next to the coastlines, where frogs would  
302 have been able to establish. In contrast, frogs that might have rafted between mainland America  
303 and Galapagos, would have reached the arid Littoral and Dry zones, which are inhospitable to  
304 amphibians. Actually, evidence from palynological studies has revealed that the lower areas of  
305 the islands were even drier in the past glacial (Colinvaux 1972, Colinvaux and Schofield 1976).

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307 Three non-native frogs<sup>2</sup> have reached the islands (Table 1):

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<sup>2</sup> The Global Invasive Species Database (GISD 2010) erroneously reported *Eleutherodactylus coqui* at Galapagos, citing Snell and Rea (1999) as the source, yet those authors reported *Scinax quinquefasciatus*.

- 309 • Jiménez-Uzcátegui et al. (2007) and Phillips et al. (2012a) reported a **Western Cane**  
310 **Toad** *Rhinella horribilis* at Galapagos (as *Bufo* sp. and *Chaunus marinus*, respectively<sup>3</sup>).  
311 Records at the Vertebrate Collection of the Charles Darwin Research Foundation  
312 (VCCDRS; CDF 2016) show that it was discovered in a house at Puerto Baquerizo  
313 Moreno, San Cristobal Island, on 5 February 1995. This species has a large native range  
314 from southern USA to the lowlands of western Ecuador and northwestern Peru (Frost  
315 2016). It inhabits a large variety of ecosystems and is abundant in anthropogenic areas  
316 like pastures and gardens (Zug and Zug 1979). Although it can live in arid environments,  
317 it depends on water availability for reproduction (see Zug and Zug 1979 for information  
318 on its natural history). *Rhinella horribilis* is present in Manta, Guayaquil and Tababela  
319 (Quito), areas with cargo warehouses, maritime ports and airports with connections to  
320 Galapagos (pers. obs.). Apparently, only one population of *Rhinella horribilis* may have  
321 established completely outside of its native range (in Florida, King and Krakauer 1966;  
322 Easteal 1981)<sup>4</sup>. No information is available on potential or evidenced impacts by non-  
323 native *R. horribilis*. For comparison, the Eastern Cane Toad *Rhinella marina* has been  
324 extensively introduced worldwide (Easteal 1981; Lever 2003), and is one of the most  
325 studied introduced species, especially in Australia. The main evidenced ecological impact  
326 of *R. marina* is the declining of Australian native predators, due to its toxicity when  
327 ingested (Shine 2010).  
328
- 329 • Snell (2000) reported an individual of **Striped Robber Frog** *Pristimantis unistrigatus*  
330 beside a dishwasher in a house on 17 March 2000 at Puerto Ayora, Santa Cruz Island.  
331 Phillips et al. (2012a) reported another *P. unistrigatus* from Isabela Island without  
332 providing further details. There are no specimens of *Pristimantis* at the VCCDRS. Frogs  
333 of the genus *Pristimantis* are part of the superfamily Brachycephaloidea (Frost 2016).  
334 Brachycephaloidean frogs are terrestrial breeders, laying their eggs on land, with no need  
335 of water, and eggs hatching directly into froglets, bypassing the tadpole stage. These  
336 features could provide clear advantages to establishing self-sufficient populations in  
337 islands with limited freshwater availability. Frogs of the Brachycephaloidean genus  
338 *Eleutherodactylus* have established spreading populations in Hawaiian and Caribbean  
339 islands, where they arrived as hitchhikers (Kraus et al. 1999; Kraus and Campbell 2002;  
340 Lever 2003; Olson et al. 2012). However, introduced populations of *Pristimantis* are

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<sup>3</sup> The correct updated name of the toad that arrived to the Galapagos is *Rhinella horribilis*, assuming its origin was western Ecuador. Until recently, *R. horribilis* was a synonym of *Rhinella marina*. However, Acevedo-Rincón et al. (2016) recognised them as different species. *Rhinella marina* is now restricted to the east of the Andes. Further taxonomic changes are expected, and populations from western Ecuador could receive yet another (new) name (Vallinoto et al. 2010).

<sup>4</sup> The non-native populations of *Rhinella* in Florida have multiple origins, with first individuals coming from Surinam and Colombia. Toads from Surinam were probably *Rhinella marina*, while those from Colombia could be *R. horribilis* if their origin was western Colombia, or *R. marina* if they came from eastern Colombia.

341 undocumented (Lever 2003, Kraus 2009), probably because most *Pristimantis* show high  
342 levels of endemism and high physiological specialisation. Nevertheless, a few species,  
343 like *P. unistrigatus*, are more widespread and have adapted to human-created habitats,  
344 showing potential to establish non-native populations if conditions for establishment are  
345 adequate. *Pristimantis unistrigatus* is native to inter-Andean highland valleys from  
346 southern Colombia to central Ecuador, where it can live in mildly arid environments with  
347 seasonal rains, and thrive in agricultural lands, gardens and other artificially watered  
348 areas (Lynch 1981). It is the most common frog in urban, suburban and rural green areas  
349 of the valley of Quito, including the surroundings of air cargo warehouses and the airport  
350 (pers. obs.).

351

- 352 • **Fowler's Snouted Treefrog *Scinax quinquefasciatus***<sup>5</sup> (Fig. 1) is the only amphibian  
353 established in the Galapagos. Snell et al. (1999) and Snell and Rea (1999) published the  
354 first reports of *S. quinquefasciatus* from Galapagos based on records from Isabela<sup>6</sup> and  
355 Santa Cruz islands. Although subsequent authors have commented on *S. quinquefasciatus*  
356 in Galapagos (Lever 2003; Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012a; Zug  
357 2013), many details about their introduction history remain unpublished. The VCCDRS  
358 (CDF 2016) holds several specimens of *S. quinquefasciatus* that offer valuable  
359 information to better contextualize its timeframe in the archipelago. The first specimen of  
360 *S. quinquefasciatus* (VCCDRS 2247) was collected on May 1973 at an unknown locality  
361 in Santa Cruz Island. Four additional specimens were collected in 1991–1992 at the dry  
362 lowlands of Santa Cruz Island, in urban areas of the town of Puerto Ayora. Between 1998  
363 and 2013, one to four specimens were obtained in or around Puerto Ayora every year,  
364 except for 2011, when 10 specimens were collected. In 2001, the first *S. quinquefasciatus*  
365 (VCCDRS 1502) was collected at humid highlands in agricultural areas of Bellavista,  
366 Santa Cruz Island, with additional single treefrogs collected in 2003, 2008, 2011 and  
367 2013. Seven treefrogs were collected in 2000 and one in 2001 in the dry lowlands of  
368 urban Puerto Baquerizo Moreno, San Cristobal Island. No further records have been  
369 reported since<sup>7</sup>. All six VCCDRS specimens of *S. quinquefasciatus* from Isabela Island  
370 were collected after its confirmed establishment at the lagoons near the town of Puerto  
371 Villamil on 1998. Since *S. quinquefasciatus* is insectivorous, predation of native  
372 invertebrate fauna has been identified as a potential impact on Galapagos biodiversity  
373 (Phillips et al. 2012a), but there are no studies regarding its diet or evidence about any  
374 real impact. *Scinax quinquefasciatus* is native to the Pacific lowlands and low montane

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<sup>5</sup> This name is currently applied to different populations of *Scinax* that include at least one undescribed cryptic species (R.W. McDiarmid in litt. 2003; S. Ron pers. comm. 2013).

<sup>6</sup> Snell and Rea (1999) confused specimens from Isabela with “leptodactylid frogs”, a common error due to the snout form and general appearance of *Scinax* frogs.

<sup>7</sup> Phillips et al. (2012) reported a “Tree frog 3 (*Hyla* sp.)” reported from San Cristobal in 1990. It is possible that it corresponds to early records of *Scinax quinquefasciatus*. Due to uncertainty with the identification and lack of voucher specimens, they are not included in these analyses.

375 areas from southwestern Colombia to central-western Ecuador (Frost 2016). In its native  
376 distribution, *S. quinquefasciatus* occurs on a variety of habitats, as it is able to breed in  
377 small ponds in agricultural areas, herbaceous marshes and stream pools in arid zones, and  
378 wetlands with low salinity in river deltas (Duellman 1971; de la Riva et al. 1997;  
379 Cisneros-Heredia 2006a; Ortega-Andrade et al. 2010; pers. obs.). It is present in urban,  
380 suburban and green rural areas of Manta and Guayaquil, including the surroundings of air  
381 cargo warehouses and the airport (pers. obs.).  
382

### 383 **Non-native reptiles in Galapagos**

384 Nine species of non-native reptiles have been recorded in Galapagos. All established populations  
385 are geckos—members of the squamate reptilian infra-order Gekkota. Worldwide, several species  
386 of geckos have adapted to live in anthropic or perianthropic conditions, dwelling in human-made  
387 buildings and surroundings. This close relationship has resulted in geckos being able to  
388 effectively colonise geographically distant regions by human-facilitated dispersion (Lever 2003,  
389 Gamble et al. 2008, Kraus 2009). Anthropophilic geckos are some of the most capable overseas  
390 dispersalists among non-volant, terrestrial vertebrates, having in some cases the largest  
391 distributions among reptiles and even attaining larger densities than in their natural habitats  
392 (Gamble et al. 2008; Ineich 2010). Presently, geckos have been introduced as non-native species  
393 far more frequently than any other lizard group (Lever 2003, Kraus 2009). Out of 503  
394 introduction events involving gekkotan species analysed by Kraus (2009), about 45% resulted in  
395 successful population establishments, showing that geckos are among the most successful  
396 reptiles in establishing populations. Not all gekkotan families are involved, and Gekkonidae,  
397 Phyllodactylidae and Sphaerodactylidae are responsible for all introduction and establishment  
398 events in the world (Lever 2003; Kraus 2009). Non-native species of the three families are  
399 present in Galapagos.  
400

- 401 • **Dwarf Gecko *Gonatodes caudiscutatus***<sup>8</sup> is found in small numbers at the town of Puerto  
402 Baquerizo Moreno<sup>9</sup>, San Cristobal Island, where it is restricted to moist anthropic  
403 environments. It is abundant in the agro-urban highlands of San Cristobal, in El Progreso,  
404 where it has been able to establish also in natural areas (Garman 1892; Wood 1939;  
405 Mertens 1963; Wright 1983; Hoogmoed 1989; Lundh 1998; Olmedo and Cayot 1994;  
406 pers. obs.). During a survey in June 2009, I found three specimens of *G. caudiscutatus* in

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<sup>8</sup> Garman (1892) described *Gonatodes collaris*, based on two specimens collected by George Baur at Wreck Bay, next to the town of Puerto Baquerizo Moreno, San Cristobal Island. Vanzolini (1965) proposed that *G. collaris* and *G. caudiscutatus* were actually synonyms, which was confirmed by Wright (1983).

<sup>9</sup> Several expeditions did not find *Gonatodes* in San Cristobal Island during the late 1800s and early 1900s (Cope 1889; Heller 1903; Van Denburgh 1912; Slevin 1935). Van Denburgh (1912), Slevin (1935) and Barbour and Loveridge (1929) suggested that the specimens reported by Garman (1892) were probably collected at Guayaquil, in mainland Ecuador. However, it is probable that *G. caudiscutatus* was overlooked due to its restricted distribution and low abundance in Puerto Baquerizo Moreno, and low activity during the dry season.

407 gardens near Playa Man and the interpretation centre, and 10 specimens at orchards in El  
408 Progreso. The rarity of *G. caudiscutatus* in the lowlands is probably due to climate  
409 restrictions and predation by domestic and native species<sup>10</sup> (Wright 1983; Hoogmoed  
410 1989; Olmedo and Cayot 1994; pers. obs.). There are reports of *G. caudiscutatus* in at  
411 least two other islands of Galapagos. Jimenez-Uzcátegui et al. (2007) reported it from  
412 Baltra, without further details. The VCCDRS (CDF 2016) has four specimens of *G.*  
413 *caudiscutatus* collected at Puerto Ayora, Santa Cruz Island: on 5 November 2003, 29  
414 January 2006, and 20 July 2006. It is probable that a small population is already  
415 established at Santa Cruz Island. Impacts by *G. caudiscutatus* on Galapagos biodiversity  
416 are unknown, but have been suspected to be slight or even non-existent (Hoogmoed  
417 1989; Olmedo and Cayot 1994; Phillips et al. 2012a). Competition or exclusion of  
418 endemic geckos is unlikely, due to body size, habitat and microhabitat differences<sup>11</sup>.  
419 Although *G. caudiscutatus* is insectivorous, it probably eats mainly non-native and  
420 widespread invertebrates, but there are no studies about its diet. *Gonatodes caudiscutatus*  
421 is native to the lowlands from central-western Ecuador and extreme northwestern Peru  
422 (Sturaro and Avila-Pires 2014). It is present in urban, suburban and green rural areas of  
423 Guayaquil, including the surroundings of air cargo warehouses and the airport (pers.  
424 obs.).

425

426 • **Peters' Leaf-toed Gecko *Phyllodactylus reissii*** arrived at Santa Cruz Island in the mid-  
427 1970s (Wright 1983, Hoogmoed 1989, Olmedo and Cayot 1994). Hoogmoed (1989)  
428 published a detailed study on the population in Puerto Ayora, where it was well  
429 established in the urban area (Hoogmoed 1989, Olmedo and Cayot 1994). Olmedo and  
430 Cayot (1994) reported one individual of *P. reissii* in natural areas next to Puerto Ayora  
431 (adjacent to Las Ninfas neighbourhood). On July 1997, I observed three *P. reissii* at the  
432 same area in natural vegetation. *Phyllodactylus reissii* has reached the highlands of Santa  
433 Cruz Island, at Bellavista (Phillips et al. 2012a). Torres-Carvajal and Tapia (2011)  
434 reported the first record of *P. reissii* at Puerto Villamil, Isabela Island, but the presence of  
435 an established population remains to be confirmed. During a survey in June 2009, I did  
436 not find *P. reissii* in San Cristobal Island. *Phyllodactylus reissii* inhabits dry forests and  
437 scrubland, and rural, suburban and urban areas from central western Ecuador to  
438 northwestern Peru (Dixon and Huey 1970). In Galapagos, *P. reissi* remains mostly  
439 restricted to urban, suburban and rural areas. In areas of Puerto Ayora where *P. reissi* is

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<sup>10</sup> I observed San Cristobal Lava Lizard *Microlophus bivittatus* predating on *G. caudiscutatus* on June 2005. See account of Domestic Chicken *Gallus gallus* for details on a predation event on *G. caudiscutatus*.

<sup>11</sup> All endemic Galapagos geckos belong to the genus *Phyllodactylus*, are diurnal and nocturnal, and inhabit the arid lowlands. They are scansorial and arboreal, having dorsoventrally compressed digits with greatly expanded lamellae. *Gonatodes caudiscutatus* has a smaller body-size than all endemic geckos, is diurnal and mainly inhabits the humid highlands. It is terrestrial and semi-arboreal, having more restricted climbing abilities than the endemic geckos due to its cylindrical digits without expanded lamellae.

440 dominant, it appears to have displaced the endemic *P. galapagensis*, and only rarely are  
441 both together (Hoogmoed 1989; Olmedo and Cayot 1994). No information about possible  
442 exclusion mechanisms or interactions has been published<sup>12</sup>. If *P. reissii* would expand to  
443 natural areas, it could impact endemic *Phyllodactylus* (Hoogmoed 1989; Olmedo and  
444 Cayot 1994; Phillips et al. 2012a).

445

446 • **Mourning Gecko *Lepidodactylus lugubris*** is native to Southeast Asia and islands of  
447 western Oceania (Hoogmoed and Avila-Pires 2015 and citations therein). It is a  
448 parthenogenetic species, which benefits the establishment of new populations (Kraus  
449 2009; Phillips et al. 2012a; Hoogmoed and Avila-Pires 2015). It has become established  
450 in north-eastern Asia, the west coast of South America, Oceania and Pacific Ocean  
451 islands, including Galapagos (Lever 2003; Kraus 2009; Hoogmoed and Avila-Pires  
452 2015). *Lepidodactylus lugubris* likely arrived to Galapagos during the early 1980s<sup>13</sup>  
453 (Hoogmoed 1989; Olmedo and Cayot 1994). It remained rare during the first decade<sup>14</sup>,  
454 but subsequently became well established and expanded. Nowadays, it has fairly large  
455 self-sustained populations, but only on moist environments in coastal areas—i.e.,  
456 artificially watered urban areas and mangroves—in the towns of Puerto Ayora, Puerto  
457 Baquerizo Moreno and Puerto Villamil (Olmedo and Cayot 1994; Sengoku 1998;  
458 Jiménez-Uzcátegui et al. 2007, 2015; Torres-Carvajal and Tapia 2011; Phillips et al.  
459 2012a; pers. obs.). It has also established in the town of El Progreso, where it remains  
460 restricted to human buildings, and has not been found in farms (M. Altamirano, in litt. 12  
461 June 2009). Jiménez-Uzcátegui et al. (2015) reported *L. lugubris* from Marchena Island,  
462 without further details. The consequences from the introduction of *L. lugubris* in  
463 Neotropical areas, incl. Galapagos, are not clear (Hoogmoed and Avila-Pires 2015). No  
464 impacts on Galapagos' biodiversity have been reported (Olmedo and Cayot 1994;  
465 Phillips et al. 2012). Competitive interactions between *L. lugubris* and Galapagos  
466 endemic geckos have apparently not affected endemic species (M. Altamirano 2002 cited  
467 in Phillips et al. 2012a). Although *L. lugubris* is insectivorous, it probably eats mainly  
468 non-native and widespread invertebrates. There are no studies yet about its diet.

469

470 • **Common House Gecko *Hemidactylus frenatus*** is a nocturnal species native to  
471 southeastern Asia (Lever 2003). It has invaded several areas across the planet, including  
472 many islands in the Indian and Pacific oceans and several areas of Africa and America,  
473 and currently has the widest worldwide non-native distribution of its genus (Lever 2003;

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<sup>12</sup> At least one study on interactions between non-native and endemic geckos in Galapagos has been conducted but remains unpublished (M. Altamirano's PhD dissertation, cited by Phillips et al. 2012).

<sup>13</sup> Hoogmoed (1989) published the first mention of *Lepidodactylus lugubris* in Galapagos. However, he did not find the species, and cited the unpublished records obtained by John Wright at Puerto Ayora, Santa Cruz Island, in 1983.

<sup>14</sup> Marinus Hoogmoed did not find *Lepidoblepharis lugubris* during his intensive surveys of Puerto Ayora in 1988 (Hoogmoed 1989; Lundh 1998).

474 Kraus 2009). Torres-Carvajal and Tapia (2011) reported the first record of *H. frenatus* in  
475 Galapagos, based on five individuals found at Puerto Villamil, Isabela Island, but an  
476 established population was not confirmed. On 24 October 2016, three *H. frenatus* were  
477 recorded at Puerto Villamil, thus suggesting that an established population is indeed  
478 present in Isabela Island (T. Schramer and Y. Kalki, in litt. 2016). It seems to have also  
479 established in Puerto Baquerizo Moreno, San Cristobal Island, where over 10 individuals  
480 were recorded between September and November 2016 in human buildings (T. Schramer  
481 and Y. Kalki, in litt. 2016). Due to its recent arrival, no information is available for any  
482 type of interactions or effects of *H. frenatus* on the endemic *Phyllodactylus* geckos.  
483 However, its arrival has raised concerns due to reported impacts on native fauna in other  
484 areas where it has established (Torres-Carvajal and Tapia 2011; Torres-Carvajal 2015).  
485 *Hemidactylus frenatus* has outcompeted and excluded non-native *Lepidodactylus*  
486 *lugubris* from several Pacific islands by competitive exclusion (Petren and Case 1998;  
487 Kraus 2009). Preliminary evidence suggests that *H. frenatus* may be also excluding *L.*  
488 *lugubris* in San Cristobal (T. Schramer and Y. Kalki, in litt. 2016). At the Mascarene  
489 Islands, *H. frenatus* contributed to the decline and population extirpation of endemic  
490 geckos of the genus *Nactus* (Cole et al. 2005). Furthermore, it could carry novel parasites  
491 that might impact native reptile species (Hoskin 2011).

492

- 493 • On 22 February 2014, a local inhabitant ran over a **Milksnake *Lampropeltis***  
494 ***micropholis***<sup>15</sup> (Fig. 2) in the area of Santa Rosa, highlands of Santa Cruz Island.  
495 Photographs of the snake were quickly disseminated through social networks and  
496 Galapagos authorities were able to recover the specimen. Four days later, the specimen  
497 was delivered and deposited at the Laboratory of Terrestrial Zoology, Universidad San  
498 Francisco de Quito USFQ, by officials of the Ministry of Environment of Ecuador MAE  
499 in order to confirm its identification and preserve it as a voucher specimen. Morphology  
500 and colouration data suggest that the specimen belongs to the population distributed in  
501 the Pacific lowlands of Ecuador. In mainland Ecuador, *L. micropholis* inhabits the Pacific  
502 lowlands and Andean highlands in a large variety of ecosystems, from arid to moist  
503 habitats (Cisneros-Heredia and Touzet 2007). *Lampropeltis micropholis* is present in the  
504 surroundings of Guayaquil<sup>16</sup> and Quito (Williams 1988; Pérez-Santos and Moreno 1991;

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<sup>15</sup> Until recently, *Lampropeltis micropholis* was a subspecies of *L. triangulum*. However, Ruane et al. (2014) raised it to species status. As currently understood, *L. micropholis* occurs from western Costa Rica to Ecuador. Further taxonomic changes are expected, and populations from the highlands of Ecuador could receive yet another (new) name (J. Valencia, in litt. 2012).

<sup>16</sup> *Lampropeltis micropholis* is rather frequent on the highlands, even in rural and suburban areas. However, there are few specimens from the lowlands (Cisneros-Heredia and Touzet 2007; pers. obs.). Williams (1988) reported it from Guayaquil, based on a specimen collected by Edward Whimper during the 1890s. Perez-Santos and Moreno (1991) reported the species from the province of Guayas, without providing details. Although no further information about *L. micropholis* from Guayaquil has been published, I am aware of two additional records: One individual collected ca. 18 km from Guayaquil and delivered to Jean-Marc Touzet (Fundación Herpetológica “Gustavo Orcés” FHGO) in February 1990

505 Cisneros-Heredia and Touzet 2007). This snake is terrestrial, active during day and night,  
506 and eats a large variety of vertebrates and invertebrates (Williams 1988). There are no  
507 records of non-native populations of *L. micropholis* established outside of its range, or  
508 studies of insular populations. For comparison, a study of the diet of insular populations  
509 of *Lampropeltis polizona* at Isabel Island, Mexico, showed that they fed on different  
510 species of terrestrial lizards and nestlings of ground-nesting marine birds, incl. Blue-  
511 footed Booby *Sula nebouxii*, but avoided arboreal geckos and tree-nesting birds. The  
512 California Kingsnake *Lampropeltis californiae* became established in Gran Canaria  
513 Island, where its main evidenced ecological impact is predation of endemic lizards  
514 (Pether and Mateo 2007; Cabrera-Pérez et al. 2012).

515

- 516 • Several individuals of **Green Iguana** *Iguana iguana* have reached the Galapagos Islands  
517 (Cruz Martínez et al. 2007; Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012a). Five  
518 specimens are deposited at the VCCDRS (CDF 2016). The earliest *I. iguana* (VCCDRS  
519 571) was collected on 15 February 1982 at an unknown locality in Santa Cruz Island.  
520 Two additional specimens were found at a private house in the town of Puerto Ayora,  
521 Santa Cruz Island, on 14 August 2000<sup>17</sup> (CDF 2016). One *I. iguana* (VCCDRS 2218)  
522 was found at an unknown locality in San Cristobal Island, on April 19<sup>th</sup>, 2008; while  
523 another (VCCDRS 2153) was found in Isabela Island on 14 June 2010 (CDF 2016). Cruz  
524 Martínez et al. (2007) and Phillips et al. (2012a) mentioned an *I. iguana* found walking in  
525 the streets of Puerto Baquerizo Moreno, San Cristobal Island. Another was photographed  
526 on a dock at Puerto Ayora on 13 August 2015 (Christen 2015). *Iguana iguana* is native  
527 from Mexico to Paraguay and southern Brazil (Uetz and Hošek 2016). It is very common  
528 on the littoral and lowlands of western Ecuador (Ortega-Andrade et al. 2010), including  
529 the surroundings of cargo warehouses and the air and maritime ports of Guayaquil (Cruz  
530 Martínez et al. 2007; pers. obs.). *Iguana iguana* is able to disperse between islands by  
531 ocean rafting (Censky et al. 1998). However, I agree with Jiménez-Uzcátegui et al. (2007,  
532 2015) and Phillips et al. (2012a) in classifying it as a non-native introduced species, as  
533 there is evidence of its hitchhiking behaviour (Cruz Martínez et al. 2007). In some islands  
534 where it has been introduced, *I. iguana* has displaced the native *I. delicatissima* by  
535 hybridisation (Lever 2003; Powell and Henderson 2005; Kraus 2009; Powell et al. 2011;  
536 Vuillaume et al. 2015). Since inter-generic hybridisation has been reported in iguanas  
537 (Rassmann et al. 1997; Jančúchová-Lásková et al. 2015), the establishment of *I. iguana*  
538 in Galapagos could pose a threat for the endemic iguanas of the genus *Amblyrhynchus*  
539 and *Conolophus*.

540

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(Touzet JM pers. comm.); and another photographed by Keyko Cruz at Cerro Blanco, ca. 8 km from Guayaquil (Cruz 2015).

<sup>17</sup> However, Jiménez-Uzcátegui et al. (2007) reported that only one *Iguana iguana* was found in Santa Cruz in 2000, while the other was found in San Cristobal.

- 541 • One **Yellow-footed Tortoise** *Chelonoidis denticulata* in Santa Cruz Island, one **Yellow-**  
 542 **spotted River Tortoise** *Podocnemis unifilis* in San Cristobal Island and a single  
 543 **Common Slider Turtle** *Trachemys scripta* in Santa Cruz and San Cristobal islands were  
 544 intercepted (Jiménez-Uzcátegui et al. 2007, 2015; Phillips et al. 2012a). All individuals  
 545 were apparently brought to Galapagos as pets, and these three species are commonly  
 546 traded as pets in mainland Ecuador (Carr and Almendáriz 1989; Cisneros-Heredia 2006b;  
 547 pers. obs.). *Chelonoidis denticulata* and *P. unifilis* are native to the Amazonian lowlands.  
 548 They are illegally caught and occasionally offered in pet stores of Quito and Guayaquil  
 549 (pers. obs.). *Trachemys scripta* is native to the western USA and Mexico and it is the  
 550 most common pet turtle and the most widely released reptile species in the world (Kraus  
 551 2009).  
 552
- 553 • A gravid **Five-lined skink** *Plestiodon inexpectatus* was intercepted as a pet in  
 554 Galapagos. Jiménez-Uzcátegui et al. (2007) and Phillips et al. (2012a) cited the island of  
 555 interception as San Cristobal. However, VCCDRS data indicate that it was intercepted at  
 556 the Baltra airport on 26 May 2005 (CDF 2016).  
 557

#### 558 **Non-native birds in Galapagos**

559 Twelve species of non-native birds have been recorded in the Galapagos Islands (Table 1):  
 560

- 561 • **Domestic ducks**<sup>18</sup>, **Domestic Turkey** *Meleagris gallopavo*, **Domestic Goose** *Anser*  
 562 *anser*, **Domestic Quail** *Coturnix japonica*<sup>19</sup>, **Domestic Guinea fowl** *Numida*  
 563 *meleagris* and **Green Peafowl** *Pavo muticus* occur in the Galapagos only in agro-urban  
 564 areas under human care (Gottdenker et al. 2005; Jiménez-Uzcátegui et al. 2007; Phillips  
 565 et al. 2012a). None of them have established self-sustaining populations outside of farms.  
 566 The 2014 Census of Agricultural Production (CGREG 2014) reported 926 ducks and 28  
 567 turkeys, all free-range, in Santa Cruz, San Cristobal and Isabela islands (Table 2). While  
 568 the number of turkeys declined by one-third when compared with the census of 2000, the  
 569 population of ducks increased by 117% (CGREG 2014).  
 570
- 571 • **Domestic Fowl or Chicken** *Gallus gallus* has been introduced across the planet as  
 572 domestic poultry, with over 21 billion reported in 2014 (FAO 2015). Several populations  
 573 have become feral, especially in the Pacific islands, incl. Galapagos (Phillips et al. 2012a;  
 574 McGowan and Kirwan 2016). The 2014 Census of Agricultural Production (CGREG

<sup>18</sup> Domestic ducks in Galapagos seem to be a mix of descendants from the Mallard *Anas platyrhynchos* and the Muscovy Duck *Cairina moschata*.

<sup>19</sup> Japanese Quail *Coturnix japonica* and Common Quail *C. coturnix* are distinct but closely related species (Johnsgard 1988; McGowan and Kirwan 2016). *Coturnix japonica* was domesticated in eastern Asia several centuries ago, and domesticated quails are derived from *C. japonica* and its hybrids with *C. coturnix* (Guyomarc'h 2003). While *C. coturnix* is a partially migratory species, the domestic *C. japonica* lost its migratory impulse during domestication (Derégnaucourt et al., 2005; Guyomarc'h, 2003).

575 2014) reported that 22,180 free-range and 70,750 intensive poultry chickens were in  
576 Galapagos. Domestic Chickens are found in all four inhabited islands of Galapagos:  
577 Santa Cruz, San Cristobal, Floreana and Isabela (Table 2). While Floreana Island holds  
578 the largest number per inhabitant and the greatest density in agricultural lands of free-  
579 range chicken, San Cristobal and Santa Cruz are the islands with the greatest density of  
580 free-range chickens (Table 2). Vargas and Bensted-Smith (2000), Gottdenker et al.  
581 (2005), Wiedenfield (2006) and Phillips et al. (2012a) reported feral (or semi-feral)  
582 populations of chickens established on the four inhabited islands. However, it remains  
583 unclear if those populations are indeed self-sufficient and truly feral—i.e., completely  
584 independent of human care.

585  
586 The main potential impact of Domestic Chicken on native fauna is the spreading of  
587 infectious diseases to native birds (Wikelski et al. 2004; Gottdenker et al. 2005;  
588 Hernandez-Divers et al. 2008; Soos et al. 2008; GISD 2010; Deem et al. 2012). Yet, this  
589 threat has not been demonstrated and the evidence remains theoretical and correlative  
590 (GISD 2010; Baker et al. 2014). The Global Invasive Species Database (GISD 2010)  
591 mentions that *G. gallus* could negatively impact native vertebrates, but their only  
592 reference (Varnham, 2006) is anecdotal and based on a different species (Green  
593 Junglefowl *Gallus varius*). Phillips et al. (2012) noted: “no impacts [by *G. gallus*] to the  
594 [Galapagos] native biota have been documented”.

595  
596 I present here the first evidence of predation on squamate reptiles by Domestic Chickens  
597 in Galapagos. On June 2009, I observed a hen attacking a small Galapagos Racer  
598 *Pseudalsophis biserialis* in a private yard next to the road between Puerto Baquerizo  
599 Moreno and El Progreso, San Cristobal Island. The hen pecked on the snake’s head and  
600 body, after which it seized the snake with its beak and started to run, chased by another  
601 hen. Eventually, the hens carrying the snake took cover inside a shed. In July, 2009, I  
602 observed a hen chasing a small Dwarf Gecko *Gonatodes caudiscutatus*, apparently found  
603 while foraging among some leaf litter and rocks in a private yard at El Progreso, San  
604 Cristobal Island. The gecko managed to flee and hide under rocks. In July 1997, I  
605 observed a rooster pecking and eating a dead Peters' Leaf-toed Gecko *Phyllodactylus*  
606 *reissi* in a vacant urban lot at Santa Cruz Island.

607  
608 *Gallus gallus* mainly eats seeds and other plant material, although it is an omnivorous  
609 bird. Red Junglefowl, the wild ancestor of the Domestic Chicken, occasionally eats  
610 lizards and snakes (Ali and Ripley 1980). Reports of attacks and predation on squamate  
611 reptiles by Domestic Chicken are rare but worldwide (Guthrie 1932, Bell 1996; Powell  
612 and Henderson 2008; Mesquita et al. 2009; Sasa et al. 2009; pers. obs.). Scarcity of  
613 records would suggest that chicken predation on lizards and snakes is an opportunistic yet  
614 atypical behaviour. However, it could also be due to under-reporting and paucity of

615 herpetologists surveying chicken yards. Free-range chickens can move over hundreds of  
616 meters away from their shelters to forage, usually towards hedges and borders where  
617 encounters with small snakes and lizards would be more prone to occur, though  
618 remaining unwitnessed.

619

620 • **Four Domestic Pigeon *Columba livia*** were brought to Floreana Island during the early  
621 1970s to establish a dovecote (Harmon et al. 1987). Within the next decade, pigeons were  
622 introduced to Santa Cruz, San Cristobal and Isabela islands (Harmon et al. 1987). The  
623 population increased rapidly, and ca. 550 pigeons were present in Galapagos by 2001—  
624 most of them semi-feral or feral (Phillips et al. 2003). The main potential impact of  
625 Domestic Pigeon on Galapagos fauna was the spreading of the protozoan parasite  
626 *Trichomonas gallinae* to the endemic Galapagos Dove *Zenaida galapagoensis* (Harmon  
627 et al. 1987; Phillips et al. 2003). Indirect evidence for this threat was anecdotal and  
628 correlative, based on the presence of the parasite in *Z. galapagoensis* on islands where  
629 pigeons occurred (and their absence in pigeon-free islands), and the decline of *Z.*  
630 *galapagoensis* on islands populated by pigeon (Baker et al. 2014; Wikelski et al. 2004). In  
631 2000, on the basis of the precautionary principle, Galapagos National Park Service and  
632 Charles Darwin Research Station started an eradication program (Phillips et al. 2012b).  
633 *Columba livia* was declared eradicated from Galapagos in 2007 (Phillips et al. 2012b).

634

635 • **Red-masked Parakeet *Psittacara erythrogenys*** was reported from Puerto Baquerizo  
636 Moreno, San Cristobal Island, in April 1996 (Vargas 1996, as *Aratinga erythrogenys*).  
637 Vargas (1996) obtained reports from local inhabitants of the presence of two or three  
638 parakeets, and he observed one *P. erythrogenys* flying between the town and the  
639 surrounding natural areas. These parakeets were possibly escaped pets and probably did  
640 not establish, and they have not been reported since (Wiedenfeld 2006; Phillips et al.  
641 2012a). *Psittacara erythrogenys* is endemic to central-western Ecuador and south-  
642 western Peru, where it inhabits deciduous and semi-deciduous forest (Ridgely and  
643 Greenfield 2001). It is among the most common birds illegally caught and traded (Juniper  
644 and Parr 1998), and freed pets can be found almost anywhere in Ecuador (pers. obs.).  
645 There are self-sustained non-native populations of *P. erythrogenys* in Spain and the USA.

646

647 • **Smooth-billed Ani *Crotophaga ani*** has naturally<sup>20</sup> expanded its distribution from South  
648 America to southern Florida, the Caribbean and Central America during the 20th century  
649 (Terborgh and Faaborg 1973; Terborgh et al. 1978; Quinn and Startek-Foote 2000; Payne  
650 and Kirwan 2016). Humans apparently introduced *C. ani* in the Galapagos Islands as a  
651 possible biological control against ticks (Harris 1973; Grant and Grant 1997; Phillips et

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<sup>20</sup> *Crotophaga ani* expansion across America has not been mediated by humans. The species is not listed within the GISD (2010).

652 al. 2012a)<sup>21</sup>. The first records of *C. ani* in Galapagos were in 1962, at Isabela Island. It  
653 progressively expanded to all major islands of the archipelago (Harris 1973; Grant and  
654 Grant 1997; Wiedenfeld 2006; Connett et al. 2013). At present, the estimated population  
655 of *C. ani* in Galapagos is over 250,000 individuals (Connett et al. 2013). *Crotophaga ani*  
656 is mainly insectivorous, but it also consumes plant material (especially fruits) and  
657 vertebrates (incl. lizards, snakes, frogs, birds and mice) (Bent 1940; Skutch 1959;  
658 Olivares and Munves 1973; Rosenberg et al. 1990; Burger and Gochfeld 2001; Payne and  
659 Sorensen 2005; Repenning et al. 2009; Connett et al. 2013). Predation on animal material  
660 seems to increase during the breeding period, which coincides with the wet season, when  
661 *C. ani* apparently prefers grasshoppers and other orthopterans (Davis 1940; Payne and  
662 Sorensen 2005; Repenning et al. 2009). Hymenopteran insects, such as euglossine bees  
663 and social wasps *Polystes* spp., have been reported as part of the diet of *Crotophaga ani*  
664 (Skutch 1959; Rosenberg et al. 1990; Raw 1997; Burger and Gochfeld 2001; Repenning  
665 et al. 2009). Two studies on the diet of *C. ani* at the Santa Cruz Island showed the  
666 presence of hymenopterans. Rosenberg et al. (1990) reported hymenopterans in only 4 of  
667 24 dissected gizzards. Connett et al. (2013) found 12 *X. darwini* in the gizzards of 12 *C.*  
668 *ani*, but in this case, it was the single most frequent invertebrate species.

669

670 Four potential impacts by *Crotophaga ani* on Galapagos biodiversity have been  
671 postulated (Rosenberg et al. 1990; Grant and Grant 1997, Dvorak et al. 2004; Fessl et al.  
672 2010):

- 673 (i) Propagation of invasive plants. Available evidence suggests that *Crotophaga ani*  
674 has a high potential to propagate introduced plants, including the invasive  
675 Raspberry *Rubus niveus* and Wild-sage *Lantana camara* (Guerrero and Tye  
676 2011).
- 677 (ii) Predation on native fauna. Rosenberg et al. (1990), Guerrero and Tye (2011), and  
678 Connett et al. (2013) reported predation of Galapagos native invertebrates, lizards  
679 and Darwin Finch nestlings by *Crotophaga ani*.
- 680 (iii) Competition with native avifauna, which remains untested and speculative.
- 681 (iv) Introduction of avian diseases, also untested and speculative.

682 Nonetheless, Phillips et al. (2012a; *contra* Rosenberg et al. 1990) stated that the Smooth-  
683 billed Ani is “a low priority alien species, not having been attributed with any serious  
684 impacts to native species, although it is likely that it has some effects on native [fauna]”.

685

686 I present herein information that constitutes the first evidence of a probable major impact  
687 on an endemic invertebrate due to predation by *Crotophaga ani* (Fig. 3) Between 8 and  
688 16 June 2009, I observed six groups of *C. ani* predating assiduously on Galapagos

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<sup>21</sup> Still, this introduction hypothesis remains an assumption, mainly based on the apparently low capacity of anis to self-disperse through long distances across oceans (Harris 1973; Grant and Grant 1997; Phillips et al. 2012).

689 Carpenter Bee *Xylophaga darwini* at six different locations on San Cristobal Island.  
690 Carpenter bees in high densities were foraging on blooming trees in the Dry Zone,  
691 usually near the coast. I observed one group of *C. ani* over a 30-minute period and the  
692 other five groups during 15-minute periods each. In total, the six groups consumed 661  
693 bees over the observation periods. Each bird captured an average of  $8.5 \pm 4.4$  (range = 4–  
694 15) bees per 15 minutes. *Crotophaga ani* continued preying upon bees after each  
695 observation period ended. Despite the continuous attacks, the bees did not disperse and  
696 more kept coming attracted by the flowers. Although large numbers of the non-native  
697 Social Wasp *Polistes versicolor* were also present, as well as some butterflies, *C. ani*  
698 largely ignored them.

- 699
- 700 • An individual of **Saffron Finch** *Sicalis flaveola* was intercepted in 2014 at Baltra  
701 Island's airport, where it arrived as a hitchhiker on an airplane from Quito (Jiménez-  
702 Uzcátegui et al. 2015). Interestingly, after its interception, it was returned to Quito where  
703 local staff misidentified it as a Galapagos endemic bird and sent it back to the  
704 archipelago<sup>22</sup> (Jiménez-Uzcátegui et al. 2015). In Ecuador, *S. flaveola*'s native  
705 distribution is in arid semi-open areas with scattered trees or shrubs, and agricultural  
706 areas of south-western Ecuador, both lowlands and inter-Andean highland valleys  
707 (Ridgely and Greenfield 2001). During the 21st century, *S. flaveola* started to expand  
708 along central-western lowlands and northern inter-Andean highland valleys of Ecuador  
709 (Henry 2005; Buitrón and Freile 2006; Cisneros-Heredia et al. 2015). It is now a frequent  
710 species in the valley of Quito, including the surroundings of air cargo warehouses and the  
711 airport (Cisneros-Heredia et al. 2015; pers. obs.).  
712
  - 713 • Phillips et al. (2012a) and Jiménez-Uzcátegui et al. (2015) reported an individual of  
714 **Great-tailed Grackle** *Quiscalus mexicanus* captured at the town of Puerto Ayora, Santa  
715 Cruz Island in 2010. However, there is a previous record of this grackle that remained  
716 unreported: One *Q. mexicanus* was filmed at Santa Cruz Island on May 2005 (Fig. 4).  
717 *Quiscalus mexicanus* has a broad distribution, from central USA to the Pacific coasts of  
718 Ecuador and northern Peru (Fraga 2014). It has expanded considerably its distribution  
719 along northern USA and Caribbean islands (Dinsmore and Dinsmore 1993; Wehtje 2003;  
720 Fraga 2016). *Quiscalus mexicanus* was first reported from the Caribbean islands in the  
721 mid-2000s (Mejía et al. 2009; Paulino et al. 2013; Levy 2015). Currently, it seems to be  
722 established at least in Jamaica and Hispaniola (Paulino et al. 2013; Levy 2015). Grackles  
723 have been observed to hitchhike on passenger boats (Norton 1902), and Haynes-Sutton et  
724 al. (2010) mentioned that *Q. mexicanus* probably reached Jamaica with cargo. The  
725 paucity of records of *Q. mexicanus* in islands suggests that it is a poor disperser across  
726 oceanic barriers, but cargo and passenger boats may offer aid for oceanic trips. The same

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<sup>22</sup> When it arrived to Galapagos for the second time, it was weak and died by the next day (Jiménez-Uzcátegui et al. 2015)

727 transport mechanism was probably used by *Q. mexicanus* to reach Galapagos (although  
728 this remains an assumption). Thus, I include this species as a non-native introduced  
729 species, rather than as a vagrant.

730

731 Nine species of terrestrial birds recorded at Galapagos have reached the islands most probably by  
732 natural dispersion from mainland South America in recent (historic) times<sup>23</sup>: Snowy Egret  
733 *Egretta thula*, Little Blue Heron *Egretta caerulea*, Cattle Egret *Bubulcus ibis*, Black-bellied  
734 Whistling-Duck *Dendrocygna autumnalis*, Masked Duck *Nomonyx dominicus*, Paint-billed  
735 Crake *Neocrex erythrops*, Purple Gallinule *Porphyrio martinicus*, Eared Dove *Zenaida*  
736 *auriculata*, Gray-capped Cuckoo *Coccyzus lansbergi* and Bananaquit *Coereba flaveola*  
737 (Wiedenfeld 2006; Jiménez-Uzcátegui et al. 2015). While most of these species have few records  
738 in the archipelago, the following species have become regular visitors or have established self-  
739 sufficient populations: *Egretta thula* with several records in Santa Cruz, Isabela, Floreana and  
740 San Cristobal islands (Wiedenfeld 2016; Hendrickson et al. 2015; pers. obs. at El Junco lagoon  
741 in July 2009); *Neocrex erythrops* with nesting populations in Santa Cruz and Floreana islands,  
742 and probably in San Cristobal and Isabela islands; *P. martinicus* with “with long periods of  
743 residence, bordering on being a permanent resident in recent years” (Wiedenfeld 2006), and *B.*  
744 *ibis* with breeding colonies on the main islands and widespread across the archipelago  
745 (Wiedenfeld 2006). All of these species are considered herein as native species of Galapagos.  
746 Although some of them may have established more easily due to human habitat modification,  
747 humans did not mediate in their arrival process.

748

749 *Bubulcus ibis* has been commonly identified as a non-native invasive species at the Galapagos  
750 Islands. However, its arrival to the Galapagos was not human-mediated but was instead a natural  
751 colonisation based entirely on the species’ adaptations to successfully disperse across oceanic  
752 routes. The original distribution of *B. ibis* included the south of the Iberian Peninsula and parts of  
753 sub-Saharan and meridional Africa. During the 19th century, *B. ibis* underwent an enormous  
754 expansion, and it has currently colonized all continents except Antarctica (Martínez-Vilalta and  
755 Motis 1992; Martínez et al. 2017). Its natural arrival to Galapagos was a matter of time and its  
756 establishment would have happened with or without anthropic areas, since it may inhabit  
757 swamps and mangroves. The existence of agricultural areas in Galapagos only facilitated the  
758 expansion of *B. ibis* in the archipelago. Its situation is very similar to *Neocrex erythrops*, also a  
759 recent arrival that has benefited from agricultural and other anthropic areas.

760

761

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<sup>23</sup> While all other bird species recorded as vagrants at Galapagos can be classified as oceanic wanderers or as stray boreal migrants (Wiedenfeld 2006; Jiménez-Uzcátegui et al. 2015).

762 **Discussion**

763

764 **Arrival mechanisms**

765 Eight (32%) non-native amphibians, reptiles and birds in Galapagos arrived as domestic animals,  
766 five (20%) as pets and one (4%) as (unsuccessful) biocontrol (Table 1). All domestic animals,  
767 pets and biocontrols were brought to the islands deliberately. However, most (44%) non-native  
768 amphibians, reptiles and birds reached the Galapagos Islands as hitchhikers aboard airplanes or  
769 ships, unintentionally translocated (Table 1). While data for most species is not complete, this  
770 hypothesis is supported by VCCDRS specimens of *Scinax quinquefasciatus* collected on a ship  
771 at Santa Cruz and at the airport of San Cristobal, and by *Sicalis flaveola* found inside of an  
772 airplane (CDF 2016).

773

774 Six hitchhiking species arrived to Galapagos before the quarantine inspection system began in  
775 June 2000, and nine species were first recorded afterwards. Among the hitchhikers, *Rhinella*  
776 *horribilis* is a large toad (> 70 mm in old juveniles, >100 mm in adults), thus unlikely to bypass  
777 quarantine inspections. The only known record of *R. horribilis* in Galapagos was made five years  
778 before the quarantine system began. *Lampropeltis micropholis* and *Iguana iguana* are large  
779 reptiles (> 600 mm) and both have reached Galapagos after 2000 (it is uncertain how they  
780 bypassed quarantine). In contrast, *Scinax quinquefasciatus*, *Pristimantis unistrigatus*, *Gonatodes*  
781 *caudiscutatus*, *Phyllodactylus reissii*, *Lepidodactylus lugubris*, and *Hemidactylus frenatus* are  
782 relatively small and with rather cryptic colorations (brownish). They could thus be easily  
783 overlooked during quarantine inspections, and multiple translocations could have occurred. Gill et  
784 al. (2001) reported live interception cases of *S. quinquefasciatus* (in Ecuadorian banana  
785 shipments), *L. lugubris* and *H. frenatus* in New Zealand, showing its ability to be translocated  
786 and to survive physiological stress during long trips.

787

788 Most hitchhiking species that have reached Galapagos occur in the surroundings of air and  
789 maritime ports, or of cargo warehouses. However, not all translocations come directly from ports  
790 of shipment. *Lepidodactylus lugubris* does not occur in areas with air or maritime ports in  
791 mainland Ecuador with connections to the Galapagos, incl. Manta, Guayaquil or Quito.  
792 *Lepidodactylus lugubris* was first recorded in mainland Ecuador at Esmeraldas in 1963 (Fugler  
793 1966). Currently, it inhabits along the humid lowlands and foothills of north-western Ecuador,  
794 restricted to urban and suburban areas in the provinces of Esmeraldas and Santo Domingo de los  
795 Tsachilas (Fugler 1966; Schauenberg 1968; Hoogmoed and Avila-Pires 2015). It is absent from  
796 the arid central and south-western lowlands of Ecuador. The translocation of *L. lugubris* to  
797 Galapagos was possibly achieved via horticultural cargo coming from Esmeraldas, or from other  
798 countries where the species was already present, such as Colombia or Panama<sup>24</sup>.

---

<sup>24</sup> The first specimen of *Lepidodactylus lugubris* from America was collected in Panama in 1916 (Fugler 1966; Hoogmoed and Avila-Pires 2015). G.K. Noble collected it during his trip for the Harvard Peruvian Expedition (Collection catalogue, Herpetology, Museum of Comparative Zoology, Harvard University).

799

800 Human-facilitated transportation has provided opportunities for amphibians, reptiles and birds to  
801 reach Galapagos, independent of their physiological adaptations to salinity or to long trips.  
802 However, upon arrival, they still need to withstand the arid environments of the Littoral and Dry  
803 zones, where freshwater is almost absent under natural conditions on most islands. While all  
804 non-native frogs, reptiles and birds reported in Galapagos are able to survive in arid  
805 environments to some degree, at least frogs and small geckos are still dependent of some  
806 humidity. Local and regional climate changes can have an important effect on the establishment  
807 and distribution of non-native species in Galapagos (Snell and Rea 1999). Higher rainfall during  
808 El Niño events (e.g., 1997–1998 and 2009–2010) was a major factor in the establishment of  
809 *Scinax quinquefasciatus* populations in Isabela, and for the expansion of *Crotophaga ani* (Snell  
810 and Rea 1999; Pazmiño 2011). El Niño in 1997–1998 increased environmental humidity and  
811 diluted salinity in the lagoons of Puerto Villamil, allowing *S. quinquefasciatus* to thrive. After  
812 the El Niño event of 2009–2010, *S. quinquefasciatus* was able to reach the humid agricultural  
813 areas of Bellavista (Pazmiño 2011).

814

815 Artificially watered green urban and suburban areas, such as parks and gardens, have played an  
816 important role in the establishment of non-native amphibians and reptiles in Galapagos. They can  
817 act as refuges for newly established species, providing resources for locally large populations  
818 and facilitating intra and inter-island dispersion across inhabited areas (Ineich 2010). All non-  
819 native geckos are mainly found in green urban and suburban areas. Genetic evidence from  
820 Isabela Island populations of *Scinax quinquefasciatus* (Pazmiño 2011) and recurring records of  
821 *S. quinquefasciatus* from Santa Cruz Island and *G. caudiscutatus* at San Cristobal suggest  
822 multiple introduction events for both species. Before El Niño's thrusts, these populations were  
823 apparently able to survive thanks to artificially watered green urban and suburban areas<sup>25</sup>.

824

825 Most hitchhiking amphibians and reptiles are usually translocated inside freight or dwelling  
826 within spaces and crevices of airplanes and ships. However, they can be transported inside tourist  
827 luggage too. On August 2009, a live *L. lugubris* was unintentionally translocated in my handbag  
828 from San Cristobal Island to Guayaquil. It probably entered my bag at a restaurant near the dock,  
829 since I never saw *L. lugubris* at the USFQ Galapagos campus, where I stayed. I noticed its  
830 presence after opening my bag in Guayaquil. Furthermore, this shows that non-native species  
831 translocations may work on both ways, exchanging individuals between populations of  
832 Galapagos and the continent.

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The gecko was collected just two years after the opening of the Panama Canal, and was probably translocated on boats coming from Hawaii or Oceania (Smith and Grant 1961). By 1941, *L. lugubris* had already reached Colombia (Daza et al. 2012; Hoogmoed and Avila-Pires 2015).

<sup>25</sup> In comparison with Santa Cruz Island, the area of urban and suburban gardens in San Cristobal is reduced. This limited habitat availability is apparently the reason why *Gonatodes caudiscutatus* holds small and restricted populations in the lowlands of San Cristobal, and why *Scinax quinquefasciatus* has not become established in that island (despite its first record in 2000).

833  
834 Large hitchhiking reptiles and birds can accidentally enter closed areas inside freight airplanes  
835 and ships, although they are easily detected and intercepted (like the individual of *Sicalis*  
836 *flaveola* in Galapagos). However, probably the most common hitchhiking situation takes place  
837 when large reptiles and birds stay on decks and other exterior structures of passenger and cargo  
838 ships. They can hitchhike after the ships have gone through departure port inspections, survive  
839 for several days, remain overlooked, and swim or fly towards land before the ship reaches  
840 controls in the arrival ports. *Iguana iguana* and *Quiscalus mexicanus* have likely arrived in this  
841 way to Galapagos. Several hitchhiker bird species are known to have arrived and established in  
842 islands around the world: House Sparrow *Passer domesticus* in the Canary and Maldives islands,  
843 Spanish Sparrow *Passer hispaniolensis* in the Canary Islands, Pale-billed Mina *Acridotheres*  
844 *cinereus* in Borneo island, Red-vented Bulbul *Pictonotus cafer* in the Marshall and Hawaii  
845 islands, House Crow *Corvus elegans* in the Socotra Islands and Australia and Great-tailed  
846 Grackle *Quiscalus mexicanus* in Jamaica (Haynes-Sutton et al. 2010; Lever 2005 Suleiman and  
847 Taleb 2010).

848

#### 849 **Vulnerable islands**

850 If further amphibian, reptile and bird introductions are to be stopped in Galapagos, it is important  
851 to establish the vulnerability of islands to those introductions, and to understand the general  
852 profile of potential hitchhikers.

853

854 The four populated islands are the most vulnerable to translocation of non-native species because  
855 they have: (i) established and active air and maritime ports, thus arrival mechanisms and  
856 dispersal events of non-native species are facilitated in repetitive occasions; (ii) large flux of  
857 local population and tourists, which means large amount of baggage and freight where non-  
858 native species may hide, find adequate microenvironments to survive the oceanic dispersion and  
859 be transported to different areas of the islands; (iii) human-modified environments where  
860 anthropophilic non-natives may find suitable niches.

861

862 Isabela Island is apparently the most vulnerable island to the establishment of amphibians  
863 because of its freshwater wetlands next to the city and harbor<sup>26</sup>. Santa Cruz, San Cristobal and  
864 Floreana islands have coastal lagoons with significantly more salinity than Las Diablas lagoon in  
865 Isabela (Gelin and Gravez 2002), thus amphibians probably do not become easily established.  
866 The highland moist zones of all populated islands are especially vulnerable to the introduction of  
867 non-native amphibians, reptiles and birds, due to the presence of mesic environments with  
868 extensive agro-urban areas and wetlands. Furthermore, the moist zones on the highlands of  
869 Isabela are closer to the coast, making it easy for non-native species to reach a mesic  
870 environment in which to survive and establish.

---

<sup>26</sup> The largest coastal lagoon of Isabela, Las Diablas, is next to the town of Puerto Villamil. Its low salinity levels (6–10 gL<sup>-1</sup>, Gelin and Gravez 2002) allow the reproduction of *S. quinquefasciatus*.

871

872 **Potential hitchhikers**

873 Intentionally introduced species, such as pets and domestic animals, are rather easy to detect and  
874 identify because they are usually conspicuous and recognisable. However, hitchhiking species  
875 are the real predicament of quarantine officials. Hitchhiking species are usually inconspicuous,  
876 difficult to identify and hard to find. There is not a single set of characteristics that ascertains the  
877 potential of vertebrates to become a successful hitchhiker or to become established in insular  
878 ecosystems. Several publications have reviewed and proposed different methods for predicting  
879 introduced species. Since I am analysing three different phylogenetically diverse groups of  
880 terrestrial vertebrates, I will use basic criteria for each group, which were selected after studying  
881 the following references: Kolar and Lodge (2001), Hayes and Barry (2008), Van Wilgen and  
882 Richardson (2012), Buckley and Catford (2016). I think this criteria set allows for fast and  
883 simple identification of potential species in mainland Ecuador that could hitchhike to Galapagos.  
884 A key factor for the control of hitchhiking species is that personnel at ports and crew in airplanes  
885 and ships receive training to correctly identify, restrain and handle non-native hitchhiking  
886 animals. Although the species lists provided herein could be improved, I hope they will provide  
887 valuable information for the Agency for Regulation and Control of Biosecurity and Quarantine  
888 for Galapagos (ABG), and other organisations involved in the conservation and management of  
889 the archipelago (incl., Consejo de Gobierno del Régimen Especial de Galápagos CGREG,  
890 Ministerio de Agricultura, Ganadería, Acuacultura y Pesca MAPAG, Parque Nacional Galápagos  
891 PNG, Ministerio del Ambiente MAE).

892

893 A cautionary note: some reptiles and birds from mainland Ecuador may look similar to those  
894 native to Galapagos. For example, the Galapagos endemic geckos of the genus *Phyllodactylus*  
895 could be confused with the non-native *Phyllodactylus reissii*; and the native *Setophaga petechia*  
896 has been confused in the past with the non-native *Sicalis flaveola*. Guides and manuals  
897 specifically focused on crew or control personnel should be produced to avoid confusion and  
898 reinforce control measurements.

899

900 Amphibian and reptile species with higher hitchhiking potential for Galapagos seem to be  
901 characterised by: (i) having inconspicuous colouration and small to medium body size<sup>27</sup>; (ii)  
902 being adapted to arid environments or anthropogenic areas<sup>28</sup>; (iii) occurring frequently in the

---

<sup>27</sup> Which contributes to their hard detection and improves their survivorship (Olson et al. 2012)

<sup>28</sup> Adaptation to desiccation conditions has also enhanced tolerance to salinity in some amphibians (Balinsky 1981; Wells 2007), thus making it easy for them to survive in low-salinity lagoons like Las Diablas in Isabela Island. The three species of *Scinax* that have become established in islands as cargo hitchhikers have adapted to arid environments or anthropogenic areas on their native distributions: *Scinax quinquemasciatus*, *S. x-signatus* and *S. ruber* (Breuil and Ibéné 2008; Breuil 2009; Kraus, 2009; Powell et al. 2011). The first two are also known to be adapted to breed in marshes with low salinity (Jiménez-Uzcátegui et al. 2007; Rios-López 2008; pers. obs.). It seems that *Scinax* species, which are able to adapt to open habitats, show some tolerance to salinity.

903 surroundings of cargo warehouses or in agricultural areas<sup>29</sup>; and (iv) living in the Pacific  
904 lowlands of central Ecuador, where habitats have environmental conditions similar to those  
905 found in the Galapagos<sup>30</sup>, and the main ports of freight airplanes and ships to Galapagos are  
906 located.

907  
908 In mainland Ecuador, there are six frog species matching this hitchhiker profile (Fig. 5): *Scinax*  
909 *quinquefasciatus*, *Pristimantis achatinus*, *Barycholos pulcher*, *Engystomops pustulatus*,  
910 *Trachycephalus jordani*, *T. typhoni* and *Rhinella horribilis*. While the first species is already  
911 established in Galapagos, the remaining five, if allowed to reach the archipelago, have a high  
912 probability of settling there. Furthermore, these species have additional advantages favoring their  
913 establishment in insular environments: *Pristimantis achatinus* and *B. pulcher* are terrestrial  
914 breeders with direct development; *E. pustulatus*, *S. quinquefasciatus* and *R. horribilis* are  
915 opportunistic breeders that can reproduce even in small puddles; and *E. pustulatus*, *T. jordani*  
916 and *T. typhoni* can inhabit extremely arid environments with low seasonal rainfall, similar to  
917 the lowlands of Galapagos. Live *T. jordani* have been intercepted as far away as the USA and  
918 New Zealand in banana shipments from mainland Ecuador (Hartweg 1955; Gill et al. 2001).  
919 Although large adult *R. horribilis* should be intercepted during quarantine, juveniles are small  
920 and inconspicuous. However, desiccation is a major mortality factor for juveniles (Zug and Zug  
921 1979), but if they were to find shelter and wet conditions, they could survive travelling to  
922 Galapagos. There are 11 species of squamate reptiles matching the hitchhiker profile in mainland  
923 Ecuador (Fig. 5): *Gonatodes caudiscutatus*, *Hemidactylus frenatus*, *Phyllodactylus reissii*,  
924 *Iguana iguana*, *Lampropeltis micropholis*, *Boa constrictor*, *Dipsas elegans*, *Erythrolamprus*  
925 *epinephelus*, *Mastigodryas* sp. (cf. *boddaerti*), *Mastigodryas pulchriceps* and *Oxybelis aeneus*.  
926 The first five of these species have already been recorded in Galapagos.

927  
928 Although little information is available on hitchhiker birds, at least the following features seem  
929 to profile potential hitchhiker birds to the Galapagos: (i) being adapted to arid environments or  
930 anthropogenic areas, which would allow them to survive in the lowlands of Galapagos; (ii)  
931 occurring frequently in the surroundings of main ports of freight airplanes and ships to  
932 Galapagos, with higher probability of entering closed areas inside of freight airplanes and ships  
933 or wandering around boat decks; (iii) habit of flying at least short distances over the sea, so they  
934 can reach departed ships; and (iv) adaptability to build nests within human-made structures, thus  
935 attracting reproductive adults to the ships. Since birds are active and noticeable animals, their  
936 detection and capture should be fairly easy during quarantine procedures.

937

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<sup>29</sup> Frogs that are common in these have easy access to freight or have a great chance to be packed along with horticultural products (Kraus et al. 1999).

<sup>30</sup> Species that establish successful self-sufficient populations usually come from areas that have a similar climate to the jurisdiction where they are introduced (Bomford et al. 2009).

938 To guide such training, I provide a shortlist of birds from mainland Ecuador that match the  
939 potential hitchhiker profile (Fig. 5): Eared Dove *Zenaida auriculata*, *Thaupis episcopus*, Saffron  
940 Finch *Sicalis flaveola*, Rufous-collared Sparrow *Zonotrichia capensis*, Shiny Cowbird *Molothrus*  
941 *bonariensis*, Great-tailed Grackle *Quiscalus mexicanus* and House Sparrow *Passer domesticus*.  
942 Of these birds, two have been already recorded at Galapagos and are discussed above. There are  
943 records of *Z. auriculata* at Champion islet, Santa Cruz and Baltra islands (Wiedenfeld 2006;  
944 Loranger 2012). Although all these areas are in or close to inhabited islands, their origin cannot  
945 be directly assigned to hitchhiking since this species is capable of oceanic dispersing (Baptista et  
946 al. 2013). Of all the birds herein listed, *M. bonariensis* could be a major threat if established in  
947 Galapagos. It is a brood parasite and can seriously affect bird species with small populations  
948 (Oppel et al. 2004). Its populations have expanded in the surroundings of the two air and  
949 maritime ports of Guayaquil and Quito (Cisneros-Heredia et al. 2015; Crespo-Pérez et al. 2016;  
950 pers. obs.).

951

### 952 **Effects, management and control**

953 Chickens have become the dominant domestic birds in all inhabited islands in Galapagos.  
954 Several studies have discussed the possible transmission of disease from chickens to native  
955 Galapagos fauna, its potential impacts and control measures (Wikelski et al. 2004; Gottdenker et  
956 al. 2005; Soos et al. 2008; Deem et al. 2012). Free-range (and feral) chickens seem to have some  
957 degree of predatory impacts on Galapagos fauna, as evidenced in this publication. However,  
958 chicken predation on endemic fauna is probably uncommon, because endemic snakes and lizards  
959 prefer dry lowland areas and most free-range and feral chickens occur in moist highland areas  
960 (CGREG 2014). In contrast, it is possible that chickens have significant impacts on the  
961 populations of the introduced gecko *Gonatodes caudiscutatus*, the only squamate reptile of  
962 Galapagos that occurs mainly in moist highland areas; i.e., agricultural lands at San Cristobal  
963 Island. Nevertheless, chicken predation probabilities increase in urban and suburban areas, where  
964 endemic snakes and endemic and non-native lizard and chickens co-occur.

965

966 Soos et al. (2008) suggested several regulatory and management procedures focused on  
967 preventing the spread of poultry diseases to wild birds, including the elimination or reduction of  
968 free-range chickens. To eliminate free-range farming could be impractical due to cultural, social  
969 and economical factors. A more plausible option would be to promote free-range poultry farming  
970 with biosecurity measures that reduce the interaction between chickens and wildlife. Some  
971 measures should include: well-kept fences to prevent chickens leaving the farm and to stop them  
972 from foraging on hedges and other vegetated areas; a peripheral ring without vegetation, rocks or  
973 wreckage around the fences, coops and troughs; and clean fenced-in pastures for poultry roaming  
974 to prevent attracting wildlife inside chicken yards. These and other measures must be established  
975 and reinforced with the active participation of Galapagos poultry owners and local and national  
976 authorities dealing with agricultural practices and wildlife conservation (incl., ABG, Consejo de  
977 Gobierno del Régimen Especial de Galápagos CGREG, Ministerio de Agricultura, Ganadería,

978 Acuacultura y Pesca MAPAG, Parque Nacional Galápagos PNG, Ministerio del Ambiente  
979 MAE).

980

981 Of all non-native species, *Crotophaga ani* is the only species with established, self-sufficient  
982 populations expanding into anthropic and natural areas in Galapagos. Data presented herein  
983 show that the Smooth-billed Ani *Crotophaga ani* can heavily predate on the Galapagos  
984 Carpenter Bee *Xylocopa darwini*. Large body size and slow flight of carpenter bees probably  
985 make them an easy and more nutritious prey for *C. ani*, in comparison with other similar species  
986 of invertebrates. Observations of six different groups of *C. ani* with an intensive predatory  
987 behaviour on *Xylocopa darwini* in San Cristobal Island suggest that this is not a unique habit.  
988 Furthermore, this behaviour may be widespread since *X. darwini* is known to be part of the diet  
989 of *C. ani* in Santa Cruz Island (Rosenberg et al. 1990; Connett et al. 2013). If similar patterns of  
990 predation are constant—at least during the breeding period—*C. ani* may have a severe impact on  
991 local carpenter bee populations. *Xylocopa darwini* is the only endemic bee from the archipelago  
992 (Gonzales et al. 2010, Rasmussen et al. 2012). It is a keystone pollinator species in the islands,  
993 being the most important flower visitors and responsible for the vast majority of insect  
994 pollination in Galapagos (Linsley 1966, Linsley et al. 1966, McMullen 1985, 1989, Phillip et al.  
995 2006, Chamorro et al. 2012). As a dominant and keystone pollinator, negative impacts on its  
996 populations may have significant effects on the plant-pollinator networks of the islands.

997

998 Eradication of established non-native populations is costly and rarely successful (Mack et al.  
999 2000), and control policies seem to have effects only before species are widespread (Olson et al.  
1000 2012; Pitt et al. 2012). In this context, the Agency for Regulation and Control of Biosecurity and  
1001 Quarantine for Galapagos (ABG) plays a decisive role in preventing new introductions of non-  
1002 native amphibians, reptiles and birds in Galapagos, especially hitchhikers. Furthermore, for non-  
1003 native species already established, it is important to stop new or multiple introductions of the  
1004 same species, since they will increase reproductive output and genetic diversity (Lambrinos  
1005 2004; Van Wilgen and Richardson 2012). Quarantine officers should pay particular attention to  
1006 horticultural trade and temperature-controlled freight, which because of their constant  
1007 temperatures, are non-lethal for amphibians and reptiles (Work et al. 2005). Decks and exposed  
1008 cargo on ships are another source of non-native species, especially large body-size hitchhikers  
1009 such as snakes, iguanas and birds.

1010

1011 If the eradication of non-native established species is of interest, the eradication program of  
1012 *Columba livia* is a successful but rather unique story (Phillips et al. 2012b). The success was due,  
1013 in part, to the availability of adequate and updated knowledge about the species' natural history,  
1014 distribution, ecological relationships, effects and eradication methods (Phillips et al. 2012b). In  
1015 contrast, eradication attempts of other non-native species that are poorly known have been

1016 unsuccessful, e.g., *Scinax quinquefasciatus*<sup>31</sup>. In fact, it is probable that after a non-native species  
1017 has become established and self-sufficient, management policies could be better focussed on  
1018 guiding its control rather than to “undertake the daunting (and often illusory) task of eradicating  
1019 them” (David et al. 2017).

1020  
1021 Very little information has been published about the natural history of most non-native  
1022 amphibians, reptiles and birds in their native distribution in mainland Ecuador. Knowledge on  
1023 non-native species is paramount to understand whether their control should be a conservation  
1024 goal in the archipelago, and if so, how it could be best achieved. Even the species’ identity of  
1025 some species is uncertain (e.g., *Rhinella horribilis*, *Scinax quinquefasciatus* and *Lampropeltis*  
1026 *micropholis*). Furthermore, knowledge about Galapagos populations remains in many cases  
1027 unpublished<sup>32</sup>. Most terrestrial non-native hitchhikers in the Galapagos are geckos and their  
1028 effects on Galapagos biodiversity have usually been considered as low or absent. Unfortunately,  
1029 Marinus Hoogmoed’s (1989) words are still valid today: “these are only speculations based on  
1030 few observations”. With all these restrictions, control policies are not sufficiently evidence-  
1031 based. Future research on non-native species should provide information on habitat and  
1032 microhabitat use, physiology and growth, intra-population tolerance to abiotic and biotic factors,  
1033 reproductive biology and population dynamics, diet and trophic interactions, both in Galapagos  
1034 and in its native distribution.

1035  
1036 Fundamentally, we need to rethink about how we understand, manage and prevent introductions  
1037 of non-native species. Available information about non-native terrestrial vertebrates in  
1038 Galapagos is still basic, and not enough to even understand their natural history and general  
1039 ecological patterns. We need to go beyond the paradigm that the main impact of non-native  
1040 species is framed by their direct effects on native species, i.e., direct competition or predation. It  
1041 is necessary to understand the ecosystemic effects of non-native species, for example on nutrient  
1042 dynamics and cumulative effects on food webs through trophic and non-trophic interactions  
1043 (e.g., mutualisms or ecosystem engineering). We also need more research on how native species  
1044 are evolving when confronted and living with non-native species, since often native species  
1045 rapidly evolve traits to better tolerate or exploit invaders (David et al. 2017).

1046  
1047

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<sup>31</sup> Eradication attempts by hand-capture, spraying caffeine, and increasing the salinity of the lagoons were unsuccessful (Jiménez-Uzcátegui et al. 2007; Phillips et al. 2012).

<sup>32</sup> For example, available knowledge about the populations of *Scinax quinquefasciatus* in Galapagos remains in two unpublished dissertations: Pazmiño (2011) described the genetic diversity and origin of the Galapagos populations of *S. quinquefasciatus*, and Vintimilla (2005) analysed the control potential of increasing water salinity.

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1063

1064 **References**

1065

- 1066 • Acevedo-Rincón, A.A., M. Lampo and R. Cipriani. (2016). The cane or marine toad,  
1067 *Rhinella marina* (Anura, Bufonidae): two genetically and morphologically distinct  
1068 species. *Zootaxa* 4103: 574–586.
- 1069 • Aldaz, I., Ortiz, E. and Valdebenito, H. (1997). Threatened species, a re-evaluation of the  
1070 status of eight endemic plants of the Galápagos. *Biodiversity & Conservation*, 7(1), 97-  
1071 107.
- 1072 • Ali, S. and Ripley, S.D. (1980). Handbook of the Birds of India and Pakistan together  
1073 with those of Bangladesh, Nepal, Bhutan and Sri Lanka. Volume 2: Megapodes to Crab  
1074 Plover. Second Edition. Oxford University Press: New Dehli.
- 1075 • Anderson, A., Stothert, K., Martinsson-Wallin, H., Wallin, P., Flett, I., Haberle, S.,  
1076 Heijnis, H. and Rhodes, E. (2016). Reconsidering Precolumbian Human Colonization in  
1077 the Galápagos Islands, Republic of Ecuador. *Latin American Antiquity*, 27(2), 169-183.
- 1078 • Baptista, L.F., Trail, P.W., Horblit, H.M., Bonan, A. and Boesman, P. (2013). Eared  
1079 Dove (*Zenaida auriculata*). Handbook of the Birds of the World Alive. Lynx Edicions,  
1080 Barcelona. (retrieved from <http://www.hbw.com/node/54207> on 8 May 2016).
- 1081 • Baker, J., Harvey, K.J. and French, K. (2014). Threats from introduced birds to native  
1082 birds. *Emu*, 114(1), 1-12.
- 1083 • Balinsky, J.B. (1981). Adaptation of nitrogen metabolism to hyperosmotic environment  
1084 in Amphibia. *Journal of Experimental Zoology*, 215(3), 335-350.
- 1085 • Barbour T. and Loveridge A. (1929). Typical reptiles and amphibians in the Museum of  
1086 Comparative Zoology. *Bulletin of the Musuem of Comparative Zoology* 69, 205–360.
- 1087 • Barnett, B.D. (1986). Eradication and control of feral and free-ranging dogs in the  
1088 Galapagos Islands. *Proceedings of the Twelfth Vertebrate Pest Conference*. University of  
1089 California: Davis.
- 1090 • Beebee, T.J.C. (1985). Salt tolerance of Natterjack Toad (*Bufo calamita*) eggs and larvae  
1091 from coastal and inland populations in Britain. *Journal of Herpetology* 1, 14–16.
- 1092 • Bell, B.D. (1996). Blackbird (*Turdus merula*) predation on the endemic copper skink  
1093 (*Cyclodina aenea*). *Notornis*, 43, 213-217.

- 1094 • Bell, R.C., Drewes, R.C., Channing, A., Gvoždík, V., Kielgast, J., Lötters, S., Stuart, B.L.  
1095 and Zamudio, K.R. (2015). Overseas dispersal of *Hyperolius* reed frogs from Central  
1096 Africa to the oceanic islands of São Tomé and Príncipe. *Journal of Biogeography*, 42(1),  
1097 65-75.
- 1098 • Bellard, C., Cassey, P., Blackburn, T.M. (2016). Alien species as a driver of recent  
1099 extinctions. *Biology Letters*, 12, 20150623. <http://dx.doi.org/10.1098/rsbl.2015.0623>
- 1100 • Benavides E, Baum R, Snell HM, Snell HL, Sites JW (2009). Island biogeography of  
1101 Galápagos lava lizards (Tropiduridae: Microlophus): species diversity and colonization of  
1102 the archipelago. *Evolution* 63: 1606–1626. doi: 10.1111/j.1558-5646.2009.00617.x
- 1103 • Bent, A.C. (1940). Life Histories of North American Cuckoos, Goatsuckers,  
1104 Hummingbirds and Their Allies: Orders Psittaciformes, Cuculiformes, Trogoniformes,  
1105 Coraciiformes, Caprimulgiformes and Micropodiiformes. United States National  
1106 Museum Bulletin 176: 1–506.
- 1107 • Bernabò, I., Bonacci, A., Coscarelli, F., Tripepi, M. and Brunelli, E. (2013). Effects of  
1108 salinity stress on *Bufo balearicus* and *Bufo bufo* tadpoles: Tolerance, morphological gill  
1109 alterations and Na<sup>+</sup>/K<sup>+</sup>-ATPase localization. *Aquatic Toxicology*, 132, 119-133.
- 1110 • Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004). Avian extinction  
1111 and mammalian introductions on oceanic islands. *Science* 305:1955–1958.
- 1112 • Blackburn, TM, Cassey P, Lockwood, J.L. (2009). The role of species traits in the  
1113 establishment success of exotic birds. *Global Change Biology*, 15, 2852–2860.
- 1114 • Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson,  
1115 J.R. and Richardson, D.M. (2011). A proposed unified framework for biological  
1116 invasions. *Trends in Ecology & Evolution*, 26(7), 333-339.
- 1117 • Boivin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlandson, J.M.,  
1118 Denham, T. and Petraglia, M.D. (2016). Ecological consequences of human niche  
1119 construction: Examining long-term anthropogenic shaping of global species distributions.  
1120 *Proceedings of the National Academy of Sciences*, 201525200.
- 1121 • Bomford, M., Kraus, F., Barry, S.C. and Lawrence, E. (2009). Predicting establishment  
1122 success for alien reptiles and amphibians: a role for climate matching. *Biological*  
1123 *Invasions*, 11(3), 713-724.

- 1124 • Breuil, M. (2009). The terrestrial herpetofauna of Martinique: Past, present, future.  
1125 Applied Herpetology, 6(2), 123-149.
- 1126 • Breuil, M., Ibéné, B. (2008), “Les hylidés envahissants dans les Antilles française et le  
1127 peuplement batrachologique naturel”, Bulletin de la Société Herpétologique de France,  
1128 vol. 125, 41-67.
- 1129 • Brown, J.H. and Sax, D.F. (2004). An essay on some topics concerning invasive species.  
1130 Austral Ecology, 29(5), 530–536.
- 1131 • Brown, J.H. and Sax, D.F. (2005). Biological invasions and scientific objectivity: reply to  
1132 Cassey et al. (2005). Austral Ecology, 30(4), 481–483.
- 1133 • Buckley, Y.M. and Catford, J. (2016). Does the biogeographic origin of species matter?  
1134 Ecological effects of native and non-native species and the use of origin to guide  
1135 management. Journal of Ecology, 104(1), 4-17.
- 1136 • Buitrón, G. and Freile, J.F. (2006). Registros inusuales de aves migratorias y de bosques  
1137 subtropicales en Quito, Ecuador. Cotinga, 26, 54-56.
- 1138 • Burger, J. and Gochfeld, M. (2001). Smooth-billed ani (*Crotophaga ani*) predation on  
1139 butterflies in Mato Grosso, Brazil: risk decreases with increased group size. Behavioral  
1140 Ecology and Sociobiology, 49(6), 482-492.
- 1141 • Cabrera-Pérez, M.A., Gallo-Barneto, R., Esteve, I., Patiño-Martínez, C. and López-  
1142 Jurado, L.F. (2012). The management and control of the California kingsnake in Gran  
1143 Canaria (Canary Islands): Project LIFE+ Lampropeltis. Aliens: The Invasive Species  
1144 Bulletin, Newsletter of the IUCN/SSC Invasive Species Specialist Group, 32, 20–28.
- 1145 • Calderón-Álvarez, C., Causton, C.E., Hoddle, M.S., Hoddle, C.D., van Driesche, R. and  
1146 Stanek III, E.J. (2012). Monitoring the effects of *Rodolia cardinalis* on *Icerya purchasi*  
1147 populations on the Galápagos Islands. BioControl, 57(2), 167-179.
- 1148 • Campbell, K., Donlan, C.J., Cruz, F. and Carrion, V. (2004). Eradication of feral goats  
1149 *Capra hircus* from Pinta Island, Galápagos, Ecuador. Oryx, 38(03), 328-333.
- 1150 • Capps, K.A. and Flecker, A.S. (2013). Invasive aquarium fish transform ecosystem  
1151 nutrient dynamics. Proceedings of the Royal Society of London B: Biological Sciences,  
1152 280(1769), 20131520.
- 1153 • Carmi, O., C.C. Witt, A.Jaramillo, J.P. Dumbacher. (2016). Phylogeography of the  
1154 Vermilion Flycatcher species complex: multiple speciation events, shifts in migratory

- 1155 behavior, and an apparent extinction of a Galápagos-endemic bird species. *Molecular*  
1156 *Phylogenetics and Evolution*: <http://dx.doi.org/10.1016/j.ympev.2016.05.029>
- 1157 • Carr, J.L. and Almendáriz, A. (1989). Contribución al conocimiento de la distribución  
1158 geográfica de los Quelonios del Ecuador Continental. *Revista Politécnica*, XIV (2), 75–  
1159 103.
  - 1160 • Carrión, V., Donlan, C.J., Campbell, K., Lavoie, C. and Cruz, F. (2007). Feral donkey  
1161 (*Equus asinus*) eradications in the Galápagos. *Biodiversity Conservation*, 16, 437–445.
  - 1162 • Cassey, P., Blackburn, T.M., Duncan, R.P. and Chown, S.L. (2005). Concerning invasive  
1163 species: reply to Brown and Sax. *Austral Ecology*, 30(4), 475–480.
  - 1164 • Causton, C.E., Peck, S.B., Sinclair, B.J., Roque-Albelo, L., Hodgson, C.J. and Landry, B.  
1165 (2006). Alien insects: threats and implications for conservation of Galápagos Islands.  
1166 *Annals of the Entomological Society of America*, 99(1), 121-143.
  - 1167 • CDF (2016). Charles Darwin Foundation Collections Database: Online data portal.  
1168 Charles Darwin Foundation. <http://www.darwinfoundation.org/datazone/collections/> Last  
1169 Updated 19 November 2015. Accessed: 29 April 2016.
  - 1170 • Censky, E.J., Hodge, K. and Dudley, J. (1998). Over-water dispersal of lizards due to  
1171 hurricanes. *Nature*, 395 (6702), 556-556.
  - 1172 • CGREG. (2014) Censo de Unidades de Producción Agropecuaria de Galápagos 2014.  
1173 Consejo de Gobierno del Régimen Especial de Galápagos CGREG, Ministerio de  
1174 Agricultura, Ganadería, Acuacultura y Pesca MAGAP, Instituto Nacional de Estadística y  
1175 Censos INEC.
  - 1176 • Chamorro, S., Heleno, R., Olesen, J.M., McMullen, C.K., Traveset, A. (2012).  
1177 Pollination patterns and plant breeding systems in the Galápagos: a review. *Annals of*  
1178 *Botany* 110: 1489–1501.
  - 1179 • Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds,  
1180 H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E. and Mack, M.C. (2000).  
1181 Consequences of changing biodiversity. *Nature*, 405(6783), 234-242.
  - 1182 • Chew M.K. and Carroll S.P. (2011). The invasive ideology: Biologists and  
1183 conservationists are too eager to demonize non-native species. *The Scientist*.  
1184 <http://www.the-scientist.com/?articles.view/articleNo/31143>

- 1185 • Chew M.K. and Hamilton, A.L. (2011) The rise and fall of biotic nativeness: a historical  
1186 perspective In D.M. Richardson (Ed.), Fifty years of invasion ecology: the legacy of  
1187 Charles Elton (35-47). Chichester: Blackwell Publishing.
- 1188 • Chew M.T. (2015). Ecologists, environmentalists, experts, and the invasion of the  
1189 ‘second greatest threat’. International Review of Environmental History 1: 7–4.
- 1190 • Christen, J.J. (2015). Facebook photo: [http://archive.is/2017.03.13-](http://archive.is/2017.03.13-001827/https://www.facebook.com/photo.php?fbid=10206029250063964)  
1191 [001827/https://www.facebook.com/photo.php?fbid=10206029250063964](https://www.facebook.com/photo.php?fbid=10206029250063964)
- 1192 • Cisneros-Heredia, D.F. (2006a). Amphibia, Machalilla National Park, western coastal  
1193 Ecuador. Check List 2:45-54.
- 1194 • Cisneros-Heredia, D.F. (2006b). Turtles of the Tiputini Biodiversity Station with remarks  
1195 on the diversity and distribution of the Testudines from Ecuador. Biota Neotropica, 6(1),  
1196 0-0.
- 1197 • Cisneros-Heredia, D.F. and Touzet, J.M. (2007). On the distribution and conservation of  
1198 *Lampropeltis triangulum* (Lacepede, 1789) in Ecuador. Herpetozoa, 19, 3/4: 182–183.
- 1199 • Cisneros-Heredia, D.F., Amigo, X., Arias, D., Arteaga, J., Bedoya, J., Espinosa, S.,  
1200 Montenegro, E., Nazati, G. and Carrión, J.M. (2015). Reporte del 1er Conteo Navideño  
1201 de Aves de Quito, Ecuador. Avances en Ciencias e Ingenierías, 7(2), B37–B51.
- 1202 • Clavero, M. (2014). Shifting baselines and the conservation of non-native species.  
1203 Conservation Biology, 28(5), 1434–6.
- 1204 • Clavero, M. and García-Berthou, E. (2005). Invasive species are a leading cause of  
1205 animal extinctions. TRENDS in Ecology and Evolution, 20(3), 110.
- 1206 • Cole, N. C., Jones, C. G., & Harris, S. (2005). The need for enemy-free space: the impact  
1207 of an invasive gecko on island endemics. Biological Conservation, 125(4), 467-474.
- 1208 • Colinvaux, P.A. (1972). Climate and the Galapagos islands. Nature, 240, 17-20.
- 1209 • Colinvaux, P.A. and Schofield, E. K. (1976). Historical Ecology in the Galapagos  
1210 Islands: I. A Holocene Pollen Record from El Junco Lake, Isla San Cristobal. Journal of  
1211 Ecology, 64(3), 989–1012. <http://doi.org/10.2307/2258820>
- 1212 • Connett, L., Guézou, A., Herrera, H.W., Carrión, V., Parker, P.G. and Deem, S.L. (2013).  
1213 Gizzard contents of the Smooth-billed Ani *Crotophaga ani* in Santa Cruz, Galápagos  
1214 Islands, Ecuador. Galápagos Research 68.

- 1215 • Cope, E.D. (1889). Scientific results of explorations by the US Fish Commission stamer  
1216 Albatross. No. III. Report on the batrachians and reptiles collected in 1887-'88.  
1217 Proceedings of the United States National Musum, 12, 141–147.
- 1218 • Crespo-Pérez, V., Pinto, C.M., Carrión, J.M., Jarrín-E., R.D., Poveda, C. and de Vries, T.  
1219 (2016) .The Shiny Cowbird, *Molothrus bonariensis* (Gmelin, 1789) (Aves: Icteridae), at  
1220 2,800 m asl in Quito, Ecuador. Biodiversity Data Journal, 4, e8184. DOI:  
1221 10.3897/BDJ.4.e8184
- 1222 • Crooks, J.A. (2002). Characterizing ecosystem-level consequences of biological  
1223 invasions: the role of ecosystem engineers. *Oikos*, 97(2), 153-166.
- 1224 • Cruz, F., Donlan, C.J., Campbell, K. and Carrion, V. (2005). Conservation action in the  
1225 Galapagos: feral pig (*Sus scrofa*) eradication from Santiago Island. *Biological*  
1226 *Conservation*, 121(3), 473-478.
- 1227 • Cruz, K. (2015). Milk Snake (*Lampropeltis triangulum*). iNaturalist.org.  
1228 <https://www.inaturalist.org/observations/1784122>
- 1229 • Cruz Martínez, J.D., Boada, R. and Causton, C.E. (2007). Análisis del riesgo asociado al  
1230 movimiento marítimo hacia y en el Archipiélago de Galápagos. Fundación Charles  
1231 Darwin y Dirección Parque Nacional Galápagos.
- 1232 • Daszak, P., Cunningham, A.A. and Hyatt, A.D. (2000). Emerging infectious diseases of  
1233 wildlife--threats to biodiversity and human health. *Science*, 287(5452), 443-449.
- 1234 • David, P., Thébault, E., Anneville, O., Duyck, P.F., Chapuis, E. and Loeuille, N. (2017).  
1235 Impacts of Invasive Species on Food Webs: A Review of Empirical Data. In D.A. Bohan,  
1236 A.J. Dumbrell and F. Massol (Eds.), *Advances in Ecological Research*, Volume 56, 1-60  
1237 pp. Academic Press. Doi: <http://dx.doi.org/10.1016/bs.aecr.2016.10.001>
- 1238 • Davis, M.A. (2003). Biotic globalization: does competition from introduced species  
1239 threaten biodiversity? *Bioscience*, 53(5), 481-489.
- 1240 • Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown,  
1241 J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P. and Thompson, K. (2011). Don't  
1242 judge species on their origins. *Nature*, 474(7350), 153-154.
- 1243 • Daza, J.D., Travers, S.L. and Bauer, A.M. (2012) .New records of the mourning gecko  
1244 *Lepidodactylus lugubris* (Duméril and Bibron, 1836) (Squamata: Gekkonidae) from  
1245 Colombia. *Check List*, 8 (1), 164–167.

- 1246 • De la Riva, I., Márquez, R. and Bosch, J. (1997). Description of the advertisement calls  
1247 of some South American Hylidae (Amphibia: Anura): taxonomic and methodological  
1248 consequences. *Bonner Zoologische Beiträge*, 47, 175-186.
- 1249 • Deem, S.L., Cruz, M.B., Higashiguchi, J.M. and Parker, P.G. (2012). Diseases of poultry  
1250 and endemic birds in Galápagos: implications for the reintroduction of native species.  
1251 *Animal Conservation*, 15(1), 73-82.
- 1252 • Derégnaucourt, S., Guyomarc'h, J.C. and Belhamra, M. (2005). Comparison of migratory  
1253 tendency in European quail *Coturnix c. coturnix*, domestic Japanese quail *Coturnix c.*  
1254 *japonica* and their hybrids. *Ibis*, 147(1), 25-36.
- 1255 • Didham, R.K., Tylianakis, J.M., Hutchison, M.A., Ewers, R.M. and Gemmill, N.J.  
1256 (2005). Are invasive species the drivers of ecological change? *Trends in Ecology &*  
1257 *Evolution*, 20(9), 470-474.
- 1258 • Dinsmore, J.J. and Dinsmore, S.J. (1993). Range expansion of the Great-tailed Grackle in  
1259 the 1900s. *Journal of the Iowa Academy of Science* 100, 54–59.
- 1260 • Dixon, J.R., and R.B. Huey. (1970). Systematics of the lizards of the gekkonid genus  
1261 *Phyllodactylus* of mainland South America. Los Angeles County Museum, Contributions  
1262 in Science 192: 1-78.
- 1263 • Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G. and Dickman, C.R. (2016).  
1264 Invasive predators and global biodiversity loss. *Proceedings of the National Academy of*  
1265 *Sciences*, 113(40), 11261-11265.
- 1266 • Doody, J.S., Green, B., Rhind, D., Castellano, C.M., Sims, R. and Robinson, T. (2009).  
1267 Population-level declines in Australian predators caused by an invasive species. *Animal*  
1268 *Conservation*, 12(1), 46-53.
- 1269 • Duellman, W.E. and Trueb, L. (1986). *Biology of amphibians*. New York: McGraw-Hill.
- 1270 • Duellman, W.E. (1971). The identities of some Ecuadorian hylid frogs. *Herpetologica* 27:  
1271 212–227.
- 1272 • Dukes, J.S., and Mooney, H.A. (2004). Disruption of ecosystem processes in western  
1273 North America by invasive species. *Revista Chilena de Historia Natural* 77(3), 411-437.
- 1274 • Dvorak, M., Vargas, H., Fessl, B. and Tebbich, S. (2004). On the verge of extinction: a  
1275 survey of the mangrove finch *Cactospiza heliobates* and its habitat on the Galápagos  
1276 Islands. *Oryx*, 38(2), 171-179.

- 1277 • Easteal, S. (1981). The history of introductions of *Bufo marinus* (Amphibia: Anura); a  
1278 natural experiment in evolution. *Biological Journal of the Linnean Society*, 16(2), 93-  
1279 113.
- 1280 • FAO. (2015) FAOSTAT. Statistics Division, Food and Agriculture Organization of the  
1281 United Nations. <http://faostat3.fao.org>
- 1282 • Fessl, B., Young, G.H., Young, R.P., Rodríguez-Matamoros, J., Dvorak, M., Tebbich, S.  
1283 and Fa, J.E. (2010). How to save the rarest Darwin's finch from extinction: the mangrove  
1284 finch on Isabela Island. *Philosophical Transactions of the Royal Society of London B:*  
1285 *Biological Sciences*, 365(1543), 1019-1030.
- 1286 • Fraga, R. (2016). Great-tailed Grackle (*Quiscalus mexicanus*). *Handbook of the Birds of*  
1287 *the World Alive*. Lynx Edicions, Barcelona. (retrieved from  
1288 <http://www.hbw.com/node/62287> on 8 May 2016).
- 1289 • Frias-Soler, R., Tindle, E., Espinosa Lopez, G., Blomberg, S., Studer-Thiersch, A., Wink,  
1290 M. and Tindle, R. (2014). Genetic and phenotypic evidence supports evolutionary  
1291 divergence of the American Flamingo (*Phoenicopterus ruber*) population in the  
1292 Galápagos Islands. *Waterbirds*, 37(4), 349-468.
- 1293 • Frost, D. R. 2016. *Amphibian Species of the World: an Online Reference*. Version 6.0  
1294 (Date of access). Electronic Database accessible at  
1295 <http://research.amnh.org/herpetology/amphibia/index.html>. American Museum of Natural  
1296 History, New York, USA.
- 1297 • Fugler, C.M. (1966). *Lepidodactylus lugubris* Duméril and Bibron in western South  
1298 America. *Journal of the Ohio Herpetological Society*, 5, 162.
- 1299 • Gamble, T., Bauer, A. M., Greenbaum, E., & Jackman, T. R. (2008). Out of the blue: a  
1300 novel, trans-Atlantic clade of geckos (Gekkota, Squamata). *Zoologica Scripta*, 37(4),  
1301 355-366.
- 1302 • Garman, S. (1892). The reptiles of the Galapagos Islands. From the collections of Dr.  
1303 George Baur. *Bulletin Essex Inst.* 24: 73-87.
- 1304 • Gelin A. and Gravez, V. (2002). *Knowledge and Conservation of Galapagos Islands*  
1305 *Coastal Lagoons (Ecuador)*. Basler Stiftung für Biologische Forschung, Charles Darwin  
1306 Biological Station and Galapagos National Park.

- 1307 • Gill, B.J.; Bejakovtch, D. and Whitaker, A.H. (2001). Records of foreign reptiles and  
1308 amphibians accidentally imported to New Zealand. *New Zealand Journal of Zoology*, 28:  
1309 351-359. DOI: 10.1080/03014223.2001.9518274
- 1310 • GISD (2010). *Gallus gallus*. Global Invasive Species Database. Invasive Species  
1311 Specialist Group, IUCN SSC: Gland, Switzerland.)  
1312 <http://www.iucngisd.org/gisd/species.php?sc=1661>
- 1313 • Gomez-Mestre, I., Tejedó, M., (2003). Local adaptation of an anuran amphibian to  
1314 osmotically stressful environments. *Evolution* 57, 1889–1899.
- 1315 • González, J.A., C. Montes, J. Rodríguez, and W. Tapia. (2008). Rethinking the  
1316 Galápagos Islands as a complex social-ecological system: implications for conservation  
1317 and management. *Ecology and Society* 13(2): 13.  
1318 <http://www.ecologyandsociety.org/vol13/iss2/art13/>
- 1319 • Gonzalez, V.H., Koch, J.B. and Griswold, T. (2010). *Anthidium vigintiduopunctatum*  
1320 Friese (Hymenoptera: Megachilidae): the elusive “dwarf bee” of the Galápagos  
1321 Archipelago? *Biological Invasions* 12(8): 2381-2383.
- 1322 • Gottdenker, N.L., Walsh, T., Vargas, H., Merkel, J., Jiménez, G.U., Miller, R.E., Dailey,  
1323 M. and Parker, P.G. (2005). Assessing the risks of introduced chickens and their  
1324 pathogens to native birds in the Galápagos Archipelago. *Biological Conservation*, 126(3),  
1325 429-439.
- 1326 • Grant P.R., Grant B.R. (1997). The rarest of Darwin's Finches. *Conservation Biology* 11:  
1327 119–127. DOI: 10.1046/j.1523-1739.1997.95399.x
- 1328 • Grant, P.R. and de Vries, T. (1993). The unnatural colonization of Galápagos by smooth-  
1329 billed anis (*Crotophaga ani*). *Noticias de Galápagos* 52: 21–23.
- 1330 • Guerrero, A.M. and Tye, A. (2011). Native and introduced birds of Galápagos as  
1331 dispersers of native and introduced plants. *Ornitología Neotropical*, 22(2), 207-217.
- 1332 • Guézou A, Trueman M, Buddenhagen CE, Chamorro S, Guerrero AM, et al. (2010). An  
1333 Extensive Alien Plant Inventory from the Inhabited Areas of Galápagos. *PLoS ONE* 5(4):  
1334 e10276. doi: 10.1371/journal.pone.0010276
- 1335 • Gurevitch, J. and Padilla, D.K. (2004a). Are invasive species a major cause of  
1336 extinctions? *Trends in Ecology & Evolution*, 19(9), 470-474.

- 1337 • Gurevitch, J. and Padilla, D.K. (2004b). Response to Ricciardi. Assessing species  
1338 invasions as a cause of extinction. *Trends in Ecology and Evolution*, 19(12), 620-620.
- 1339 • Guthrie, J.E. (1932). Snakes versus birds; birds versus snakes. *The Wilson Bulletin*,  
1340 44(2), 88-113.
- 1341 • Guyomarc'h, J.C. (2003). Elements for a common quail (*Coturnix c. coturnix*)  
1342 management plan. *Game & wildlife science*, 20(1-2), 1-92.
- 1343 • Harmon, W.M., Clark, W.A., Hawbecker, A.C. and Stafford, M. (1987). *Trichomonas*  
1344 *gallinae* in columbiform birds from the Galapagos Islands. *Journal of Wildlife Diseases*,  
1345 23(3), 492-494.
- 1346 • Harris, M.P. (1973). The Galápagos Avifauna. *The Condor*, 75(3), 265–278.  
1347 <http://doi.org/10.2307/1366166>
- 1348 • Hartweg, N. (1955). Division of Reptiles and Amphibians, Museum of Zoology. Pp. 24–  
1349 26. In: J. S. Rogers. Report of the Director of the Museum of Zoology 1953–1954.  
1350 University of Michigan: Ann Arbor.
- 1351 • Hayes, K.R. and Barry, S.C. (2008). Are there any consistent predictors of invasion  
1352 success? *Biological Invasions*, 10, 483–506.
- 1353 • Haynes-Sutton, A., Downer, A. and Sutton, R. (2010). A photographic guide to the birds  
1354 of Jamaica. Christopher Helm, A&C Black Publishers: London.
- 1355 • Hedges, S.B., Hass, C.A. and Maxson, L.R. (1992). Caribbean biogeography: molecular  
1356 evidence for dispersal in West Indian terrestrial vertebrates. *Proc. Natl. Acad. Sci. USA*  
1357 89: 1909-1913.
- 1358 • Heller E. (1903). Papers from the Hopkins Stanford Galapagos Expedition, 1898–1899.  
1359 XIV. Reptiles. *Proceedings of the Washington Academy of Sciences* 5, 39–98.
- 1360 • Hendrickson J., Goria-Hendrickson, K., and Woodleaf Legacy Birding Team. (2015).  
1361 Checklist S24779522: San Cristóbal-El Junco Lagoon, Galápagos, EC. eBird.  
1362 <http://ebird.org/ebird/view/checklist?subID=S24779522>.
- 1363 • Henry, P.Y. (2005). New distributional records of birds from Andean and western  
1364 Ecuador. *Cotinga*, 23, 27-32.
- 1365 • Hernandez-Divers, S.M., Villegas, P., Jimenez, C., Hernandez-Divers, S.J., Garcia, M.,  
1366 Riblet, S.M., Carroll, C.R., O'Connor, B.M., Webb, J.L., Yabsley, M.J. and Williams,

- 1367 S.M. (2008). Backyard chicken flocks pose a disease risk for neotropical birds in Costa  
1368 Rica. *Avian diseases*, 52(4), 558-566.
- 1369 • Hoeck, P.E., Bollmer, J.L., Parker, P.G. and Keller, L.F. (2010). Differentiation with  
1370 drift: a spatio-temporal genetic analysis of Galápagos mockingbird populations (*Mimus*  
1371 spp.). *Philosophical Transactions of the Royal Society of London B: Biological Sciences*,  
1372 365(1543), 1127-1138.
- 1373 • Hoffmann, B.D. and Courchamp, F. (2016). Biological invasions and natural  
1374 colonisations: are they that different? *NeoBiota* 29: 1–14.
- 1375 • Hoogmoed M.S. (1989). Introduced geckos in Puerto Ayora, Santa Cruz, with remarks on  
1376 other areas. *Noticias de Galápagos* 47, 12–16.
- 1377 • Hoogmoed, M. S., & Avila-Pires, T. C. (2015). *Lepidodactylus lugubris* (Duméril &  
1378 Bibron 1836)(Reptilia: Gekkonidae), an introduced lizard new for Brazil, with remarks  
1379 on and correction of its distribution in the New World. *Zootaxa*, 4000(1), 90-110.
- 1380 • Hoskin, C.J. (2011). The invasion and potential impact of the Asian House Gecko  
1381 (*Hemidactylus frenatus*) in Australia. *Austral Ecology*, 36, 240–251.
- 1382 • Ineich, I. (2010). How habitat disturbance benefits geckos: Conservation implications.  
1383 *Comptes Rendus Biologies*, 333(1), 76-82.
- 1384 • IUCN/SSC (2013). Guidelines for Reintroductions and other Conservation  
1385 Translocations. Version 1.0. Gland: IUCN Species Survival Commission.
- 1386 • Jackson, M.H. (1993). Galápagos, a natural history. Calgary: University of Calgary Press.
- 1387 • Jančúchová-Lásková, J., Landová, E. and Frynta, D. (2015) Are genetically distinct lizard  
1388 species able to hybridize? A review. *Current Zoology*, 61 (1), 155–180.
- 1389 • Jaramillo, M., Donaghy-Cannon, M., Vargas, F.H. and Parker, P.G. (2016). The Diet of  
1390 the Galápagos Hawk (*Buteo galapagoensis*) Before and After Goat Eradication. *Journal*  
1391 *of Raptor Research*, 50(1), 33-44.
- 1392 • Jiménez-Uzcátegui, G., Carrión, V., Zabala, J., Buitrón, P. and Milstead, B. (2007).  
1393 Status of introduced vertebrates in Galápagos. Galápagos Report 2006–2007. Puerto  
1394 Ayora: Charles Darwin Foundation, pp. 136–141.
- 1395 • Jiménez-Uzcátegui, G., Zabala, J., Milstead, B., Snell, H.L. (2015). CDF Checklist of  
1396 Galápagos Introduced Vertebrates. Charles Darwin Foundation: Puerto Ayora,

- 1397 Galápagos: [http://www.darwinfoundation.org/datazone/checklists/introduced-](http://www.darwinfoundation.org/datazone/checklists/introduced-species/introduced-vertebrates/)  
1398 [species/introduced-vertebrates/](http://www.darwinfoundation.org/datazone/checklists/introduced-species/introduced-vertebrates/) Last updated: 23 Sep 2015. Accessed 19 Apr 2016.
- 1399 • Johnsgard, P.A. (1988) *The Quails, Partridges, and Francolins of the World*, Oxford  
1400 Univ. Press, Oxford.
- 1401 • Josse, C. (2001). *La biodiversidad del Ecuador: informe 2000*. Quito: Ministerio del  
1402 Ambiente de Ecuador, EcoCiencia, UICN. 368 pp.
- 1403 • Juniper, T. and M. Parr. (1998). *Parrots: a guide to parrots of the world*. Yale University  
1404 Press, New Haven, Connecticut.
- 1405 • King, W. and Krakauer, T. (1966). The exotic herpetofauna of southern Florida.  
1406 *Quarterly Journal of the Florida Academy of Sciences*, 29, 144-154.
- 1407 • Kolar, C.S. and Lodge, D.M. (2001). Progress in invasion biology: predicting invaders.  
1408 *Trends in Ecology & Evolution*, 16(4), 199–204.
- 1409 • Konecny, M.J. (1987). Food Habits and Energetics of Feral House Cats in the Galápagos  
1410 Islands. *Oikos*, 50(1), 24–32. <http://doi.org/10.2307/3565398>
- 1411 • Kraus, F. (2009). *Alien Reptiles and Amphibians: A Scientific Compendium and*  
1412 *Analysis*. *Invading Nature, Springer Series in Invasion Ecology, Volume 4*.
- 1413 • Kraus, F. and Campbell, E.W. (2002). Human-mediated escalation of a formerly  
1414 eradicable problem: the invasion of Caribbean frogs in the Hawaiian Islands. *Biological*  
1415 *Invasions*, 4, 327–332.
- 1416 • Kraus, F., Campbell, E.W., Allison, A. and Pratt, T. (1999). *Eleutherodactylus* Frog  
1417 introduction to Hawaii. *Herpetological Review*, 30(1), 21-25.
- 1418 • Kuebbing SE and Simberloff D (2015). Missing the bandwagon: Nonnative species  
1419 impacts still concern managers. *NeoBiota* 25: 73-86. doi: 10.3897/neobiota.25.8921
- 1420 • Lambrinos, J.G. (2004). How interactions between ecology and evolution influence  
1421 contemporary invasion dynamics. *Ecology*, 85(8), 2061-2070.
- 1422 • Lever, C. (2003). *Naturalized Reptiles and Amphibians of the World*. New York: Oxford  
1423 University Press.
- 1424 • Lever, C. (2005). *Naturalised birds of the world*. T&AD Poyser, A&C Black Publishers:  
1425 London.
- 1426 • Levy, C. (2015). Great-tailed Grackle (*Quiscalus mexicanus*) spreading in Jamaica.  
1427 *Journal of Caribbean Ornithology*, 28, 15–16.

- 1428 • Linsley EG, Rick CM, Stephens SG. (1966). Observations on the floral relationships of  
1429 the Galápagos carpenter bee. *The Pan-Pacific Entomologist* 42: 1–18.
- 1430 • Linsley, EG (1966). Pollinating insects of the Galápagos Islands. pp. 225-232 In R.I.  
1431 Bowman (ed.) *The Galápagos: Proceedings of the Symposia of the Galápagos*  
1432 *International Scientific Project*. University of California Press, Berkeley. 318 p.
- 1433 • Lomolino, M.V., Riddle, B.R., Whittaker, R.J. and Brown, J.H. (2010). *Biogeography*.  
1434 Sunderland, MA: Sinauer Associates. 878 pp.
- 1435 • Loope, L.L.; Hamann, O. and Stone, C.P. (1988). Comparative conservation biology of  
1436 oceanic archipelagoes. *Hawaii and the Galápagos*. *Bioscience* 38: 272-282.
- 1437 • Loranger, J. (2012). Checklist S18646809: Isla Baltra, Galápagos, EC. eBird.  
1438 <http://ebird.org/ebird/view/checklist?subID=S18646809>
- 1439 • Lundh, J.P. (1998). Insidious Invaders. *Noticias de Galápagos*, 59, 33–34.
- 1440 • Lynch, J.D. (1981). Leptodactylid frogs of the genus *Eleutherodactylus* in the Andes of  
1441 Northern Ecuador and adjacent Colombia. *The University of Kansas, Museum of Natural*  
1442 *History, Miscellaneous Publications* 72:1-46
- 1443 • MacDougall, A.S. and Turkington, R. (2005). Are invasive species the drivers or  
1444 passengers of change in degraded ecosystems? *Ecology*, 86(1), 42-55.
- 1445 • Mace, G., Masundire, H., Baillie, J., et al. (2005). Biodiversity. Pp. 77–122. In: Hassan,  
1446 R., Scholes, R., Ash, N. (Eds). *Ecosystems and human well-being: current state and*  
1447 *trends*. Volume 1. *The Millennium Ecosystem Assessment*. Washington, D.C.: Island  
1448 Press.
- 1449 • Mack, R.N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M. and Bazzaz, F.A.  
1450 (2000). Biotic invasions: causes, epidemiology, global consequences, and control.  
1451 *Ecological applications*, 10(3), 689-710.
- 1452 • MacLeod, A., Rodríguez, A., Vences, M., Orozco-terWengel, P., García, C., Trillmich,  
1453 F., Gentile, G., Caccone, A., Quezada, G. and Steinfartz, S. (2015). Hybridization masks  
1454 speciation in the evolutionary history of the Galápagos marine iguana. *Proceedings of the*  
1455 *Royal Society B: Biological Sciences*, 282 (1809), 20150425.
- 1456 • Maddock, S.T., Day, J.J., Nussbaum, R.A., Wilkinson, M. and Gower, D.J. (2014).  
1457 Evolutionary origins and genetic variation of the Seychelles treefrog, *Tachycnemis*

- 1458 *seychellensis* (Duméril and Bibron, 1841) (Amphibia: Anura: Hyperoliidae). Molecular  
1459 Phylogenetics and Evolution, 75, 194-201.
- 1460 • Martínez-Vilalta A. and Motis, A. (1992). Family Ardeidae (Hérons), p. 376-429. In: J.  
1461 del Hoyo, A. Elliott and J. Sargatal (eds) Handbook of the Birds of the World, v. 1.  
1462 Barcelona: Lynx Editions.
- 1463 • Martínez-Vilalta, A., Motis, A. and Kirwan, G.M. (2017). Cattle Egret (*Bubulcus ibis*).  
1464 In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). Handbook  
1465 of the Birds of the World Alive. Lynx Edicions, Barcelona. (retrieved from  
1466 <http://www.hbw.com/node/52697>).
- 1467 • Mauchamp, A. (1997). Threats from Alien Plant Species in the Galápagos Islands.  
1468 Conservation Biology, 11(1), 260–263.
- 1469 • McGeoch, M.A. and Latombe, G. (2016). Characterizing common and range expanding  
1470 species. Journal of Biogeography, 43, 217–228.
- 1471 • McGowan, P.J.K. and Kirwan, G.M. (2015). Red Junglefowl (*Gallus gallus*). Handbook  
1472 of the Birds of the World Alive. Lynx Edicions, Barcelona. (retrieved from  
1473 <http://www.hbw.com/node/53485> on 8 May 2016).
- 1474 • McGowan, P.J.K. and Kirwan, G.M. (2016). Japanese Quail (*Coturnix japonica*).  
1475 Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. (retrieved from  
1476 <http://www.hbw.com/node/53433> on 9 May 2016).
- 1477 • McLean, E.B., White, A.M. and Matson, T.O. (1995). Smooth-billed Ani (*Crotophaga*  
1478 *ani* L.), a New Species of Bird for Ohio. The Ohio Journal of Science 95(5): 335–336.
- 1479 • McMullen CK. (1985). Observation on insect visitors to flowering plants of Island Santa  
1480 Cruz. Part I. The endemic carpenter bee. Noticias de Galápagos 42: 24-25.
- 1481 • McMullen, C.K. (1989). The Galápagos Carpenter Bee, just how important is it?  
1482 Noticias de Galápagos 48: 16-18.
- 1483 • Measey, G.J., Vences, M., Drewes, R. C., Chiari, Y., Melo, M. and Bourles, B. (2007).  
1484 Freshwater paths across the ocean: molecular phylogeny of the frog *Ptychadena newtoni*  
1485 gives insights into amphibian colonization of oceanic islands. Journal of Biogeography,  
1486 34(1), 7-20.

- 1487 • Mejía, D.A., Paulino, M.M., Wallace, K. and Latta, S.C. (2009). Great-tailed Grackle  
1488 (*Quiscalus mexicanus*): a new species for Hispaniola. *Journal of Caribbean Ornithology*,  
1489 22, 112–114.
- 1490 • Mertens R. (1963). Die Wiederentdeckung der Geckonengattung *Gonatodes* auf den  
1491 Galapagos. *Senckenbergiana Biologia* 44, 21–23.
- 1492 • Mesquita, P.C.M.D., Passos, D.C., Borges-Nojosa, D.M. and Bezerra, C.H. (2009).  
1493 *Apostolepis cearensis* (Gomes' Burrowing Snake). *Diet. Herpetological Review* 40(4):  
1494 440.
- 1495 • Norton, A.H. (1902). The Boat-tailed Grackle as a stow-away. *The Auk*, 19(3), 289–290.
- 1496 • O'Connor, J.A., Sulloway, F.J., Robertson, J. and Kleindorfer, S. (2010). *Philornis*  
1497 *downsi* parasitism is the primary cause of nestling mortality in the critically endangered  
1498 Darwin's medium tree finch (*Camarhynchus pauper*). *Biodiversity and Conservation*,  
1499 19(3), 853-866.
- 1500 • O'Dowd, D.J., Green, P.T. and Lake, P.S. (2003). Invasional 'meltdown' on an oceanic  
1501 island. *Ecology Letters*, 6(9), 812-817.
- 1502 • Olivares, A. and Munves, J.A. (1973). Predatory Behavior of Smooth-Billed Ani. *The*  
1503 *Auk*, 891-891.
- 1504 • Olmedo, L.J. and Cayot, L.J. (1994). Introduced geckos in the towns of Santa Cruz, San  
1505 Cristobal and Isabela. *Noticias de Galapagos* 53: 7-12.
- 1506 • Olson, C.A., Beard, K.H. and Pitt, W. C. (2012). Biology and Impacts of Pacific Island  
1507 Invasive Species. 8. *Eleutherodactylus planirostris*, the Greenhouse Frog (Anura:  
1508 Eleutherodactylidae) 1. *Pacific Science*, 66(3), 255-270.
- 1509 • Opiel, S., Schaefer, H.M., Schmidt, V. and Schröder, B. (2004). Cowbird parasitism of  
1510 pale-headed Brush-finch *Atlapetes pallidiceps*: implications for conservation and  
1511 management. *Bird Conservation International*, 14, 63–75.
- 1512 • Ortega-Andrade, H.M.; Meza-Ramos, P.; Cisneros-Heredia, D.F.; Yáñez-Muñoz, M.H.;  
1513 Altamirano-Benavides, M. (2010). Los anfibios y reptiles del Chocó Esmeraldeño. In:  
1514 MECN. Serie Herpetofauna del Ecuador: El Chocó Esmeraldeño. Museo Ecuatoriano de  
1515 Ciencias Naturales: Quito.

- 1516 • Parent, C.E. and Crespi, B.J. (2006). Sequential colonization and diversification of  
1517 Galápagos endemic land snail genus *Bulimulus* (Gastropoda, Stylommatophora).  
1518 Evolution, 60(11), 2311-2328.
- 1519 • Paulino, M.M., Mejía, D.A. and Latta, S.C. (2013). First record of Great-tailed Grackle  
1520 (*Quiscalus mexicanus*) breeding in the West Indies. Journal of Caribbean Ornithology,  
1521 26, 63–65.
- 1522 • Payne, R. and Kirwan, G.M. (2016). Smooth-billed Ani (*Crotophaga ani*). Handbook of  
1523 the Birds of the World Alive. Lynx Edicions, Barcelona. (retrieved from  
1524 <http://www.hbw.com/node/54907> on 6 May 2016).
- 1525 • Payne, R.B. and Sorensen, M.D. (2005). The Cuckoos. Oxford University Press: Oxford.
- 1526 • Pazmiño, D.A. (2011). Origen de las poblaciones introducidas de *Scinax*  
1527 *quinquefasciatus* (Anura:Hylidae) en las islas Galápagos. Tesis de Licenciatura,  
1528 Pontificia Universidad Católica del Ecuador: Quito.
- 1529 • Pejchar, L. and Mooney, H.A. (2009). Invasive species, ecosystem services and human  
1530 well-being. Trends in Ecology & Evolution, 24(9), 497-504.
- 1531 • Pereyra, P.J. (2016). Revisiting the use of the invasive species concept: An empirical  
1532 approach. Austral Ecology. DOI: 10.1111/aec.12340
- 1533 • Pérez-Santos, C. and Moreno, A. G. (1991). Serpientes de Ecuador. Monografie di  
1534 Museo Regionale di Scienze Naturali, Torino; 11: 1–538.
- 1535 • Pether, J. and Mateo, J.A. (2007) La culebra real (*Lampropeltis getulus*) en Gran Canaria,  
1536 otro caso preocupante de reptil introducido en el Archipiélago Canario. Boletín de la  
1537 Asociación Herpetológica Española, 18: 20–23.
- 1538 • Petren, K. and Case, T.J. (1998). Habitat structure determines competition intensity and  
1539 invasion success in gecko lizards. Proceedings of the National Academy of Sciences of  
1540 the United States of America 95: 11739–11744.
- 1541 • Phillip, M., Böcher, J., Siegismund, H.R., Nielsen, L.R. (2006). Structure of a plant-  
1542 pollinator network on a pahoehoe lava desert of the Galápagos Islands. Ecography 29:  
1543 531-540.
- 1544 • Phillips, R.B., Cooke, B.D., Carrión, V. and Snell, H.L. (2012b). Eradication of rock  
1545 pigeons, *Columba livia*, from the Galápagos Islands. Biological Conservation, 147(1),  
1546 264-269.

- 1547 • Phillips, R.B., Snell, H.L. and Vargas, H. (2003). Feral rock doves in the Galápagos  
1548 Islands: Biological and economic threats. *Noticias de Galápagos*, 62, 6-11.
- 1549 • Phillips, R.B., Wiedenfeld, D.A. and Snell, H.L. (2012a). Current status of alien  
1550 vertebrates in the Galápagos Islands: invasion history, distribution, and potential impacts.  
1551 *Biological Invasions*, 14(2), 461-480.
- 1552 • Pitt, W.C.; Beard, K.H.; Doratt, R.E. (2012). Management of Invasive Coqui Frog  
1553 Populations in Hawaii. *Outlooks on Pest Management*, 23(4), 166–169.
- 1554 • Poulakakis N, Russello M, Geist D, Caccone A (2012). Unravelling the peculiarities of  
1555 island life: vicariance, dispersal and the diversification of the extinct and extant giant  
1556 Galápagos tortoises. *Mol Ecol* 21: 160–173. doi: 10.1111/j.1365-294X.2011.05370.x
- 1557 • Powell, R. and Henderson, R.W. (2005). Conservation status of Lesser Antillean reptiles.  
1558 *Iguana*, 12(2), 63-77.
- 1559 • Powell, R. and Henderson, R.W. (2008). Avian predators of West Indian reptiles. *Iguana*,  
1560 15, 8-11.
- 1561 • Powell, R., Henderson, R.W., Farmer, M.C., Breuil, M., Echternacht, A.C., van Buurt,  
1562 G., Romagosa, C.M. and Perry, G. (2011). Introduced amphibians and reptiles in the  
1563 greater Caribbean: Patterns and conservation implications. *Conservation of Caribbean*  
1564 *island herpetofaunas*, 1, 63-143.
- 1565 • Preston, C.D., Pearman, D.A. and Hall, A.R. (2004). Archaeophytes in Britain. *Botanical*  
1566 *Journal of the Linnean Society*, 145, 257–294.
- 1567 • Pyšek, P., Hulme, P.E. and Nentwig, W. (2009). Glossary of the Main Technical Terms  
1568 Used in the Handbook. In DAISIE. *Handbook of Alien Species in Europe* (375–379).  
1569 Springer Science+Business Media B.V.
- 1570 • Quinn, J.S. and Startek-Foote, J.M. (2000). Smooth-billed Ani (*Crotophaga ani*). The  
1571 *Birds of North America Online* (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology.  
1572 <http://bna.birds.cornell.edu/bna/species/539>. DOI:10.2173/bna.539
- 1573 • Rahman, S.C. and Das, K. (2013). *Amphiesma stolatum* (Striped Keelback). Predation.  
1574 *Herpetological Review* 44(1): 151.
- 1575 • Rasmussen, C., Carrion, A.L., Castro-Urgal, R., Chamorro, S., Gonzalez, V.H., Griswold,  
1576 T.L., Herrera, H.W., McMullen, C.K., Olesen, J.M. and Traveset, A. (2012). *Megachile*  
1577 *timberlakei* Cockerell (Hymenoptera: Megachilidae): Yet another adventive bee species

- 1578 to the Galápagos Archipelago. *The Pan-Pacific Entomologist* 88(1): 98–102. doi:  
1579 10.3956/2012-04.1
- 1580 • Rassmann, K., Trillmich, F. and Tautz, D. (1997). Hybridization between the Galápagos  
1581 land and marine iguana (*Conolophus subcristatus* and *Amblyrhynchus cristatus*) on Plaza  
1582 Sur. *Journal of Zoology*, 242(4), 729-739.
  - 1583 • Raw, A. (1997). Avian predation on individual neotropical social wasps (Hymenoptera,  
1584 Vespidae) outside their nests. *Ornitologia Neotropical*, 8, 89-92.
  - 1585 • Repenning, M., Basso, H.C. P., Rossoni, J.R., Krügel, M.M. and Fontana, C.S. (2009).  
1586 Análise comparativa da dieta de quatro espécies de cucos (Aves: Cuculidae), no sul do  
1587 Brasil. *Zoologia (Curitiba)* 26(3), 443-453. [https://dx.doi.org/10.1590/S1984-](https://dx.doi.org/10.1590/S1984-46702009000300008)  
1588 [46702009000300008](https://dx.doi.org/10.1590/S1984-46702009000300008)
  - 1589 • Ricciardi, A. (2004). Assessing species invasions as a cause of extinction. *Trends in*  
1590 *Ecology and Evolution*, 19(12), 619.
  - 1591 • Ricciardi, A. (2007). Are modern biological invasions an unprecedented form of global  
1592 change? *Conservation Biology* 21:329–336.
  - 1593 • Ricciardi, A., Hoopes, M.F., Marchetti, M.P. and Lockwood, J.L. (2013). Progress  
1594 toward understanding the ecological impacts of nonnative species. *Ecological*  
1595 *Monographs*, 83(3), 263-282.
  - 1596 • Ridgely, R.S. and Greenfield, P.J. (2001). *The birds of Ecuador*. Ithaca, NY: Cornell  
1597 University Press.
  - 1598 • Riofrío-Lazo M and Páez-Rosas D (2015). Feeding Habits of Introduced Black Rats,  
1599 *Rattus rattus*, in Nesting Colonies of Galápagos Petrel on San Cristóbal Island,  
1600 Galápagos. *PLoS ONE* 10(5): e0127901. doi: 10.1371/journal.pone.0127901
  - 1601 • Rios-López, N. (2008). Effects of increased salinity on tadpoles of two anurans from a  
1602 Caribbean coastal wetland in relation to their natural abundance. *Amphibia-Reptilia*,  
1603 29(1), 7-18.
  - 1604 • Rodríguez, M.C. and Drummond, H. (2000). Exploitation of avian nestlings and lizards  
1605 by insular milksnakes, *Lampropeltis triangulum*. *Journal of Herpetology*, 139-142.
  - 1606 • Rosenberg, D.K., Wilson, M.H. and Cruz, F. (1990). The distribution and abundance of  
1607 the smooth-billed ani *Crotophaga ani* (L.) in the Galápagos Islands, Ecuador. *Biological*  
1608 *Conservation*, 51(2), 113-123.

- 1609 • Ruane, S., Bryson, R.W., Pyron, R.A. and Burbrink, F.T. (2014). Coalescent species  
1610 delimitation in milksnakes (genus *Lampropeltis*) and impacts on phylogenetic  
1611 comparative analyses. *Systematic Biology*, 63: 231–250.
- 1612 • Russell, J.C. and Blackburn, T.M. (2017). The rise of invasive species denialism. *Trends*  
1613 *in Ecology & Evolution*, 32(1), 3-6.
- 1614 • Sasa, M., Wasko, D.K. and Lamar, W.W. (2009). Natural history of the terciopelo  
1615 *Bothrops asper* (Serpentes: Viperidae) in Costa Rica. *Toxicon*, 54(7), 904-922.
- 1616 • Schauenberg, P. (1968). Sur la presence de *Lepidodactylus lugubris* (Duméril & Bibron,  
1617 1836) (Reptilia, Gekkonidae) en Equateur. *Revue Suisse de Zoologie*, 76 (12), 415–417.
- 1618 • Schofield, E.K. (1989). Effects of introduced plants and animals on island vegetation:  
1619 examples from Galápagos Archipelago. *Conservation Biology*, 3(3), 227-239.
- 1620 • Sengoku, S. (1998). *Lepidodactylus lugubris* (Mourning Gecko). Ecuador: Galapagos  
1621 Islands: Isla Santa Cruz in Puerto Ayora. *Herpetological Review*, 29(2), 110.
- 1622 • Sequeira AS, Sijapati M, Lanteri AA, Roque Albelo L (2008). Nuclear and mitochondrial  
1623 sequences confirm complex colonization patterns and clear species boundaries for  
1624 flightless weevils in the Galápagos archipelago. *Philos T Roy Soc B* 363: 3439–3451.  
1625 doi: 10.1098/rstb.2008.0109
- 1626 • Shiels, A.B. and Drake, D.R. (2011). Are introduced rats (*Rattus rattus*) both seed  
1627 predators and dispersers in Hawaii?. *Biological Invasions*, 13(4), 883-894.
- 1628 • Shine, R. (2010). The ecological impact of invasive cane toads (*Bufo marinus*) in  
1629 Australia. *The Quarterly Review of Biology*, 85(3), 253-291.
- 1630 • Simbana, W. and Tye, A. (2009). Reproductive biology and responses to threats and  
1631 protection measures of the total population of a critically endangered Galápagos plant,  
1632 *Linum cratericola* (Linaceae). *Botanical Journal of the Linnean Society*, 161(1), 89-102.
- 1633 • Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J.,  
1634 Courchamp, F., Galil, B., García-Berthou, E., Pascal, M. and Pyšek, P. (2013). Impacts of  
1635 biological invasions: what's what and the way forward. *Trends in ecology & evolution*,  
1636 28(1), 58-66.
- 1637 • Skutch, A.F. (1959). Life history of the Groove-billed Ani. *The Auk* 76, 281-317.
- 1638 • Slevin, J.R. (1935). An account of the reptiles inhabiting the Galápagos Islands. *Bulletin*  
1639 *New York Zoological Society* 38: 1-24.

- 1640 • Smith, H.M. and Grant, C. (1961) The mourning gecko in the Americas. *Herpetologica*,  
1641 17 (1), 68.
- 1642 • Snell, H. and Rea, S. (1999). The 1997–98 El Niño in Galápagos: can 34 years of data  
1643 estimate 120 years of pattern. *Noticias de Galápagos*, 60, 11-20.
- 1644 • Snell, H.L. (2000). Second new frog found in Galapagos. *Galápagos News* 10: 8.
- 1645 • Snell, H.L., C. Marquez, and M. Altamirano. (1999). A new inhabitant of Galapagos.  
1646 *Galapagos News* 8: 1–2.
- 1647 • Snell, H.M., P.A. Stone and H. L. Snell. (1996). A Summary of Geographical  
1648 Characteristics of the Galapagos Islands. *Journal of Biogeography*, 23(5): 619–624.
- 1649 • Sol, D. (2016). Progresses and controversies in invasion biology. In R. Mateo et al. (eds).  
1650 *Current Trends in Wildlife Research, Wildlife Research Monographs* 1. pp. 177-200.  
1651 Springer International Publishing.
- 1652 • Soos, C., Padilla, L., Iglesias, A., Gottdenker, N., Bédon, M.C., Rios, A. and Parker, P.G.  
1653 (2008). Comparison of pathogens in broiler and backyard chickens on the Galápagos  
1654 Islands: implications for transmission to wildlife. *The Auk*, 125(2), 445-455.
- 1655 • Sturaro, M.J. and Avila-Pires, T.C.S. (2013). Redescription of the gecko *Gonatodes*  
1656 *caudiscutatus* (Günther, 1859) (Squamata: Sphaerodactylidae). *South American Journal*  
1657 *of Herpetology*, 8(2), 132–145.
- 1658 • Suleiman, A.S. and N. Taleb. (2010). Eradication of the House Crow *Corvus splendens*  
1659 on Socotra, Yemen. *Sandgrouse*, 32(2), 136–140.
- 1660 • Terborgh, J. and Faaborg, J. (1973). Turnover and ecological release in the avifauna of  
1661 Mona Island, Puerto Rico. *The Auk*, 90(4), 759-779.
- 1662 • Terborgh, J., Faaborg, J., and Brockmann, H.J. (1978). Island colonization by Lesser  
1663 Antillean birds. *The Auk*, 59-72.
- 1664 • Torres-Carvajal O (2015). On the origin of South American populations of the common  
1665 house gecko (Gekkonidae: *Hemidactylus frenatus*). *NeoBiota* 27: 69–79.
- 1666 • Torres-Carvajal, O. and Tapia, W. (2011). First record of the common house gecko  
1667 *Hemidactylus frenatus* Schlegel, 1836 and distribution extension of *Phyllodactylus reissii*  
1668 Peters, 1862 in the Galápagos. *CheckList*, 7(4).
- 1669 • Torres-Carvajal, O., Barnes, C.W., Pozo-Andrade, M.J., Tapia, W. and Nicholls, G.  
1670 (2014). Older than the islands: origin and diversification of Galápagos leaf-toed geckos

- 1671 (Phyllodactylidae: Phyllodactylus) by multiple colonizations. *Journal of Biogeography*,  
1672 41(10), 1883-1894.
- 1673 • Tye, A. (2006). Can we infer island introduction and naturalization rates from inventory  
1674 data? Evidence from introduced plants in Galápagos. *Biological Invasions*, 8(2), 201-215.
- 1675 • Tye, A., Soria, M.C. and Gardener, M.R. (2002). A strategy for Galápagos weeds. Pp.  
1676 336-341. In: Veitch, CR and MN Clout. (Eds). *Turning the tide: the eradication of*  
1677 *invasive species*. IUCN Species Specialist Group. IUCN, Gland Switzerland and  
1678 Cambridge, UK.
- 1679 • Uetz, P. and Hošek, J. (2016). *The Reptile Database*. Version 17 April 2016.  
1680 <http://www.reptile-database.org>. Accessed 26 April 2016.
- 1681 • Vallinoto, M., F. Sequeira, D. Sodr , J.A.R. Bernardi, I. Sampaio, and H. Schneider.  
1682 (2010). Phylogeny and biogeography of the *Rhinella marina* species complex (Amphibia,  
1683 Bufonidae) revisited: implications for Neotropical diversification hypotheses. *Zoologica*  
1684 *Scripta* 39: 128–140.
- 1685 • Van Denburgh, J. (1912). The geckos of the Galapagos Archipelago. Expedition of the  
1686 California Academy Sciences to the Galapagos Island 1905-1906. *Proceedings of the*  
1687 *California Academy Sciences*, 4<sup>th</sup> series 1: 405-430.
- 1688 • Van Der Wal, R., Fischer, A., Selge, S. and Larson, B.M. (2015). Neither the public nor  
1689 experts judge species primarily on their origins. *Environmental Conservation*, 42(04),  
1690 349-355.
- 1691 • Van Wilgen, N.J. and Richardson, D.M. (2012). The Roles of Climate, Phylogenetic  
1692 Relatedness, Introduction Effort, and Reproductive Traits in the Establishment of Non-  
1693 Native Reptiles and Amphibians. *Conservation Biology*, 26(2), 267-277.
- 1694 • Vanzolini, P.E. (1965). On the *Gonatodes* of the Galapagos Islands (Sauria, Gekkonidae).  
1695 *Pap is Avulsos de Zoologia* 17(2): 17-19.
- 1696 • Vargas, H. (1996). What is happening with the avifauna of San Crist bal? *Noticias de*  
1697 *Gal pagos* 57: 23–24.
- 1698 • Vargas, H. and Bensted-Smith, R. (2000). Past and present ornithology in Gal pagos. In:  
1699 N. Sitwell, L. Baert and G. Cuppois (eds). *Proceedings of the Symposium Science and*  
1700 *Conservation in Galapagos*. *Bulletin de l'Institut Royal des Sciences Naturelles de*  
1701 *Belgique* 70: 47-52.

- 1702 • Varnham, K. (2006) Non-native species in UK Overseas Territories: a review. JNCC  
1703 Report 372. Joint Nature Conservation Committee: Peterborough.  
1704 <http://jncc.defra.gov.uk/page-3660>
- 1705 • Vences, M., Kosuch, J., Rödel, M.O., Lötters, S., Channing, A., Glaw, F. and Böhme, W.  
1706 (2004). Phylogeography of *Ptychadena mascareniensis* suggests transoceanic dispersal in  
1707 a widespread African-Malagasy frog lineage. *Journal of Biogeography*, 31(4), 593-601.
- 1708 • Vences, M., Vieites, D.R., Glaw, F., Brinkmann, H., Kosuch, J., Veith, M. and Meyer, A.  
1709 (2003). Multiple overseas dispersal in amphibians. *Proceedings of the Royal Society B*  
1710 *Biological Sciences*, 270, 2435–2442.
- 1711 • Vitousek, P.M., D'antonio, C.M., Loope, L.L., Rejmanek, M. and Westbrooks, R. (1997).  
1712 Introduced species: a significant component of human-caused global change. *New*  
1713 *Zealand Journal of Ecology*, 1-16.
- 1714 • Vuillaume, B., Valette, V., Lepais, O., Grandjean, F. and Breuil, M. (2015). Genetic  
1715 Evidence of Hybridization between the endangered native species *Iguana delicatissima*  
1716 and the invasive *Iguana iguana* (Reptilia, Iguanidae) in the Lesser Antilles: Management  
1717 Implications. *PLoS ONE* 10(6): e0127575. doi: 10.1371/journal.pone.0127575
- 1718 • Wehtje, W. (2003). The range expansion of the Great-tailed Grackle (*Quiscalus*  
1719 *mexicanus* Gmelin) in North America since 1880. *Journal of Biogeography* 30(10),  
1720 1593–1607.
- 1721 • Wells, K.D. (2007). *The Ecology & Behavior of Amphibians*. The University of Chicago  
1722 Press: Chicago and London.
- 1723 • Wiedenfeld, D.A. (2006). Aves, the Galápagos Islands, Ecuador. *Check List*, 2(2), 1-27.
- 1724 • Wiggins, I.L. and D.M. Porter. (1971). *Flora of the Galápagos Islands*. Stanford  
1725 University Press. Stanford, USA.
- 1726 • Wikelski, M., J. Foufopoulos, H. Vargas, and H. Snell. (2004). Galápagos Birds and  
1727 Diseases: Invasive Pathogens as Threats for Island Species. *Ecology and Society* 9(1): 5.  
1728 <http://www.ecologyandsociety.org/vol9/iss1/art5/>
- 1729 • Williams, K.L. (1988). Systematics and natural history of the American milksnake,  
1730 *Lampropeltis micropholis*. 2nd Ed. Milwaukee Pub. Mus., Milwaukee, Wisconsin.

- 1731 • Wilson, J.R., Dormontt, E.E., Prentis, P.J., Lowe, A.J., and Richardson, D.M. (2009).  
1732 Something in the way you move: dispersal pathways affect invasion success. *Trends in*  
1733 *Ecology & Evolution*, 24(3), 136-144.
- 1734 • Wood G.C. (1939). Results of the Pinchot South Sea Expedition, III. Galapagos reptiles.  
1735 *Notulae Naturae* 15:1–4.
- 1736 • Work, T.T., McCullough, D.G., Cavey, J.F. and Komsa, R. (2005). Arrival rate of  
1737 nonindigenous insect species into the United States through foreign trade. *Biological*  
1738 *Invasions*, 7, 323 – 332.
- 1739 • Wright, J.W. (1983). The distribution and status of *Gonatodes collaris* in the Galápagos  
1740 Archipelago. *Herpetological Review* 14(1): 32.
- 1741 • Young, A.M. and Larson, B.M. (2011). Clarifying debates in invasion biology: a survey  
1742 of invasion biologists. *Environmental Research*, 111(7), 893–898.
- 1743 • Zug, G.R. (2013). Reptiles and amphibians of the Pacific Islands: a comprehensive guide.  
1744 Univ of California Press.
- 1745 • Zug, G. R. & Zug, P. B. (1979). The marine toad, *Bufo marinus*: a natural history resume  
1746 of native populations. *Smithsonian Contributions to Zoology*, 284, 1–58.
- 1747
- 1748

1749 **TABLE 1. List of non-native amphibians, reptiles and bird species in the Galápagos Islands.**

1750

Suprataxa	Family	Genus	Species	Establishment Status	Biogeographic Origin	Arrival method	Islands
Amphibia	Bufo	<i>Rhinella</i>	<i>marina</i>	Non-established	Non-native	Human mediated	San Cristóbal
Amphibia	Hylidae	<i>Scinax</i>	<i>quinquefasciatus</i>	Incipient	Non-native	Human mediated	Santa Cruz, San Cristóbal, Isabela
Amphibia	Craugastoridae	<i>Pristimantis</i>	<i>unistrigatus</i>	Non-established	Non-native	Human mediated	Santa Cruz, Isabela
Squamata	Colubridae	<i>Lampropeltis</i>	<i>micropholis</i>	Non-established	Non-native	Human mediated	Santa Cruz
Squamata	Sphaerodactylidae	<i>Gonatodes</i>	<i>caudiscutatus</i>	Incipient	Non-native	Human mediated	Santa Cruz, San Cristobal, Baltra
Squamata	Gekkonidae	<i>Lepidodactylus</i>	<i>lugubris</i>	Successful	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela, Marchena
Squamata	Gekkonidae	<i>Hemidactylus</i>	<i>frenatus</i>	Newly established	Non-native	Human mediated	Isabela
Squamata	Phyllodactylidae	<i>Phyllodactylus</i>	<i>reissii</i>	Dispersed	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Squamata	Iguanidae	<i>Iguana</i>	<i>iguana</i>	Non-established	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Squamata	Scincidae	<i>Plestiodon</i>	<i>inexpectatus</i>	Non-established	Non-native	Human mediated	San Cristobal
Testudines	Bataguridae	<i>Trachemys</i>	<i>scripta</i>	Non-established	Non-native	Human mediated	Santa Cruz, San Cristobal
Testudines	Pelomedusidae	<i>Podocnemis</i>	<i>unifilis</i>	Non-established	Non-native	Human mediated	San Cristobal
Testudines	Testunidae	<i>Chelonoidis</i>	<i>denticulata</i>	Non-established	Non-native	Human mediated	Santa Cruz
Aves	Anatidae	<i>Anas/Cairina</i>	<i>platyrhynchos/moschata</i>	Domestic	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Aves	Anatidae	<i>Anser</i>	<i>anser</i>	Domestic	Non-native	Human mediated	Santa Cruz, San Cristobal

Aves	Columbidae	<i>Columba</i>	<i>livia</i>	Eradicated	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Aves	Cuculidae	<i>Crotophaga</i>	<i>ani</i>	Successful	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela, Floreana, Genovesa, Marchena, Pinta, Pinzon, Santiago
Aves	Phasianidae	<i>Coturnix</i>	<i>japonica</i>	Domestic	Non-native	Human mediated	Santa Cruz
Aves	Phasianidae	<i>Gallus</i>	<i>gallus</i>	Domestic   Dispersed	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela, Baltra
Aves	Phasianidae	<i>Meleagris</i>	<i>gallopavo</i>	Domestic	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Aves	Phasianidae	<i>Numida</i>	<i>meleagris</i>	Domestic	Non-native	Human mediated	Santa Cruz, San Cristobal, Isabela
Aves	Phasianidae	<i>Pavo</i>	<i>muticus</i>	Domestic	Non-native	Human mediated	San Cristobal
Aves	Icteridae	<i>Quiscalus</i>	<i>mexicanus</i>	Non-established	Non-native	Human mediated	Santa Cruz
Aves	Thraupidae	<i>Sicalis</i>	<i>flaveola</i>	Non-established	Non-native	Human mediated	Baltra
Aves	Psittacidae	<i>Aratinga</i>	<i>erythrogenys</i>	Non-established	Non-native	Human mediated	San Cristobal

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1753 **TABLE 2.** Free-range Domestic Chicken *Gallus gallus* in the Galapagos Islands based on data reported by the 2014 Census of  
 1754 Agricultural Production (CGREG 2014). Free-range chickens were defined as those allowed to move freely in outdoors. Census did  
 1755 not include areas where stock was raised entirely for self-consumption, thus total numbers might be slightly underestimated.  
 1756

Island	Number of ducks	Number of turkeys	Number of free-range chicken	Chickens per 100 inhabitants	Density in agricultural lands: Chickens per 1 km <sup>2</sup> of agricultural land	Density in the whole island: Chicken per 10 km <sup>2</sup> of total land area
Santa Cruz	407	3	10340	57	108	105
San Cristobal	328	21	7286	86	131	131
Isabela	191	4	3973	147	110	9
Floreana	0	0	581	387	253	34

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1759 **TABLE 3.** Topology to evaluate the degree of establishment of non-native amphibians, reptiles  
 1760 and birds in Galapagos, independent of their conservation effects. It is based on McGeoch and  
 1761 Latombe (2016), with some modifications.

1762

<b>Category</b>	<b>Degree of expansion</b>	<b>Population size</b>	<b>Time since establishment</b>
Non-established	Intercepted	None	None
Domestic	Human-dependant	Human-dependant	Recent/Historic
Newly established	Narrow	Small	Recent
Incipient	Narrow	Large	Recent
Dispersed	Wide	Small	Recent
Successful	Wide	Large	Recent
Eradicated	Wide/Narrow	None	Recent/Historic
Non-common	Narrow	Small	Historic
Constrained	Narrow	Large	Historic
Sparse	Wide	Small	Historic
Highly Successful	Wide	Large	Historic

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1764 FIGURE 1. Juvenile of *Scinax quinefasciatus* at Santa Cruz Island, Galapagos. Photo: Luke  
1765 Smith.



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1767

1768 FIGURE 2. Specimen of *Lampropeltis micropholis* collected at Santa Rosa, Santa Cruz Island,  
1769 Galapagos.  
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1774 FIGURE 3. *Crotophaga ani* predating on Galapagos Carpenter Bee *Xylocopa darwini*. Photo by  
1775 Zell Lundberg and Christina Mitchell.



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1778 FIGURE 4. *Quiscalus mexicanus* at Santa Cruz Island, Galapagos, on May 2005. Photo by Kevin  
1779 Dowie (www.kevindowie.com)



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1782 FIGURE 5. Species of amphibians, reptiles and birds from mainland Ecuador that could be  
 1783 potential hitchhikers in the Galapagos islands.  
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