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Current status of alien vertebrates in the Galápagos Islands: invasion history, distribution, and potential impacts

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Abstract Human activity has promoted the invasion of the Galápagos Islands by alien species from each of the five classes of vertebrates. We review the current distribution of alien vertebrates in the archipelago, their impacts on native species, and management efforts aimed at alien vertebrates. A total of 44 species have been reported in the archipelago, with 20 species establishing feral populations. Mammals were the first group arriving in the archipelago and remain the most numerous, with 10 established species. Alien birds invaded after mammals and four species have established populations. Reptiles, amphibians, and fish invaded later and are represented by three, one, and two species, respectively. Alien mammals are the most injurious to native biota, contributing to the decline or extinction of several species. Aside from mammals, no other class of alien vertebrate has had documented impacts on native species. Several populations of large

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and medium-sized mammals and birds have been eradicated.

Keywords Alien impacts · Alien vertebrates · Galápagos Islands · Invasion history · Review

Introduction

The Galápagos Islands are unique among tropical and temperate islands having remained undiscovered by humans until 1535 and essentially unsettled until the 1830s (Perry 1984). The archipelago is recognized as a World Heritage Site and a biodiversity hotspot (Myers et al. 2000) because of the high degree of endemism of its plant and animal species. In contrast to many of the world's archipelagos, the ecological integrity of the Galápagos is largely intact and relatively few extinctions have occurred (Tye et al. 2002).

Alien species are one of the principal threats to global biodiversity (Vitousek et al. 1997) and insular ecosystems have proven exceptionally susceptible to invasion by aliens and vulnerable to their negative effects (Courchamp et al. 2003; O'Dowd et al. 2003; Blackburn et al. 2004). Despite the relatively brief human occupation, hundreds of alien species, representing a wide variety of taxa, have invaded the Galápagos Islands. More than 750 alien plants occur in the Galápagos, outnumbering native plant species (Tye 2006; Guézou et al. 2010) and alien insects

number almost 500 species, comprising one-quarter of the total invertebrate fauna (Causton et al. 2006). Though far fewer in number, alien vertebrates were among the earliest invaders and have had some of the most devastating effects on the Galápagos biota (MacFarland et al. 1974; Kruuk and Snell 1981; Hamann 1984; Cruz and Cruz 1987).

Numerous authors have reported on the presence and impact of alien vertebrates (primarily mammals) in the Galápagos (Eckhardt 1972; de Vries and Black 1983; Laurie 1983; Hoeck 1984). However, in the almost three decades since the last review (Hoeck's 1984), the human population has increased five-fold to more than 30,000 inhabitants and tourism has grown from around 20,000 visitors per year to an estimated 150,000 per year. Coincident with the anthropogenic changes within the Galápagos, the status of alien vertebrates has changed as well. New species have invaded the archipelago, some single-island and archipelago-wide eradications have been conducted successfully, some eradications have been attempted but failed, and several species have expanded their ranges within the archipelago. Current data on alien vertebrates exist in various forms, are widely dispersed, and largely unavailable to the scientific community. In this paper we have two objectives: (1) synthesize the available information on alien vertebrates in the Galápagos and provide a current review of chronology and distribution of species in the archipelago; and (2) assess the impact of alien vertebrates on the native biota. Our work should provide biologists and managers information to help prioritize and direct management of alien species within the Galápagos.

The Galápagos Islands

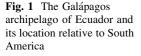
The archipelago is comprised of 129 islands and islets. For six islets we have no biogeographic data and exclude these from analyses. The remaining 123 islands range in size from 0.02 to 458,812 ha (Fig. 1; Snell et al. 1996). Most of the land area (>95%) is protected as the Galápagos National Park (GNP), with the remainder urban and agricultural. The human population in the Galápagos, estimated at 30,000–40,000 (UNESCO 2010) is dispersed across five islands: Santa Cruz, San Cristóbal, Isabela, Floreana, and Baltra (Fig. 1). Baltra is administered by the Galápagos National Park Service (GNPS), Ecuadorian

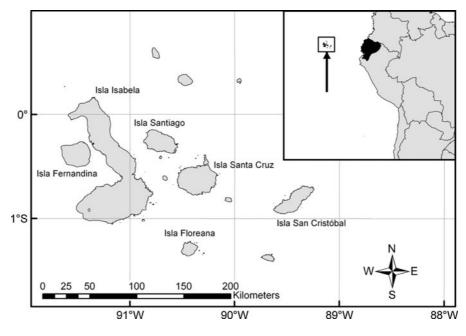
Air Force, the Ecuadorian Navy, and the Municipality of Santa Cruz. The majority of the population lives on Santa Cruz ($\sim 24,000$), San Cristóbal ($\sim 10,000$), and Isabela ($\sim 2,000$), in the urban coastal communities of Puerto Ayora, Puerto Baquerizo Moreno, and Puerto Villamil, respectively. Each island also has a small agricultural community in the highlands. Floreana was the first island settled in 1832, followed by San Cristóbal in 1869 and Isabela in 1895 (Perry 1984). In the 1920s, Santa Cruz was inhabited and Baltra in the early 1940s. Santiago had a small temporary settlement during the 1930s and 1940s. Management of the natural resources of the Galápagos is primarily the responsibility of the GNPS. Scientific research in support of the archipelago's conservation generally has been carried out by the Charles Darwin Research Station (CDRS) of the Charles Darwin Foundation and visiting scientists.

The native terrestrial vertebrate fauna of the Galápagos is comprised of three taxa: reptiles, birds, and mammals (herein we use the "traditional" nomenclature for 'reptiles' and 'birds' despite the paraphyletic grouping). No native amphibians or freshwater fish are found in the archipelago. There are 30 currently named species of native reptiles (12 tortoises, 2 snakes, 6 geckos, 7 lava lizards, 4 iguanas) in the Galápagos, excluding sea turtles (Ernst and Barbour 1989; Thomas 1997; Swash and Still 2000). Birds are the largest and most diverse native group, comprised of 64 resident and migrant species, excluding marine birds (Harris 1973; Wiedenfeld 2006). At the time of discovery, the Galápagos had nine native mammals, seven rodents and two bats, although three of the rodents are now extinct (McCracken et al. 1997; Dowler et al. 2000).

Methods

Much of the data for this paper was compiled from various published sources: peer-reviewed literature, CDRS publications (e.g. Noticias de Galápagos), and gray literature (CDRS & GNPS trip reports). Additional data are derived from the authors' previously unpublished research and observations. The authors have a combined >20 years experience in the Galápagos and have visited all islands in the archipelago. The majority of alien vertebrates are large and easily detected. Similarly, when not directly observed,





many species leave distinctive evidence (e.g. tracks and feces). For smaller less visible organisms, detection methods varied. Presence or absence of alien geckos was based on visual encounter surveys conducted in conjunction with research on native reptiles. The detection of alien rodents usually followed one of two routes: (1) while conducting unrelated field activities GNPS or CDRS field personnel would detect the presence of rodents on an island thought free of rodents. Field personnel would later trap on the island to confirm the presence or absence of rodents and to determine the species; (2) two of the authors (HLS and RBP) and visiting scientists trapped extensively in the archipelago in conjunction with management and research projects on the native and alien rodents of the Galápagos. For several species, such as frogs, first detection often was made by local inhabitants and later confirmed by GNPS or CDRS personnel.

Results

As of 2011, 44 species of alien vertebrate have been reported from Galápagos (Appendix Tables 1, 2, 3), comprising all classes (Fish, Amphibia, Reptilia, Aves, and Mammalia). Mammals are the most numerous group with 17 species reported, followed by birds, reptiles, and amphibians with 12, 9, and 4 species, respectively. Only two species of fish have

been documented. Of the total species reported, 20 have naturalized: 10 species of mammal, 4 species of bird, 3 species of reptile, 2 species of fish, and 1 species of amphibian.

Of the 123 islands in the archipelago, 55 have at least 1 alien vertebrate reported, with mammals on 46 islands and birds on 31 (Appendix Tables 2, 3). Black rats (Rattus rattus) account for most of the mammals, invading 36 islands. Feral goats (Capra hircus) are fairly widespread, having been introduced to 14 islands. Cattle egrets (Bubulcus ibis) are the most widespread bird, occurring on 25 islands. Only islands with human inhabitants (past or present) have more than 5 alien species of vertebrates per island: San Cristóbal, 35; Santa Cruz, 27; Isabela, 24; Floreana, 19; Santiago, 14; and Baltra, 9. For 30 islands the status of some alien vertebrates is unknown; some species, such as black rats may occur on these islands, but definitive surveys have not been conducted.

Account and impacts of feral and domesticated species

Fish

Nile tilapia (*Oreochromis niloticus*): In 2006, tilapia were discovered in Laguna Junco on San Cristóbal.

The exact date of introduction is unknown, but based on the largest size class of tilapia at the time of discovery it is estimated that the population was no more than 2 years old in 2006 (Toral and Poulsom 2006). The extent to which tilapia can invade freshwater habitat on San Cristóbal and other islands is self-limiting due to the scarcity of this habitat within the archipelago. However, Mozambique tilapia are tolerant of saline conditions and have invaded Fanning Atoll, Micronesia (Hensley and Courtenay 1980; Lobel 1980). Native freshwater fish are not present in Galápagos, minimizing competitive interactions. But, aquatic habitat is important for several native invertebrates, including an endemic dragonfly (Aeshna galapagoensis) and tilapia are omnivorous consuming aquatic vegetation and invertebrates (Moyle 1976; Boschung and Mayden 2004). Tilapia were eradicated from Laguna Junco in 2007 using rotenone (Nico and Walsh 2011). Surveys of Laguna Junco in 2010 indicated the eradication was successful (Leo Nico U. S. Geological Survey, personal communication). Reports from GNPS personnel in 2011 suggest tilapia may have been reintroduced to the lake, however these reports have not been verified.

Pacific fat sleeper (*Dormitator latifrons*): This fish was first reported from the Galápagos in 1992 (Massay and Mosquera 1992). To date, it has only been documented from La Laguna de las Diablas (previously known as Laguna del Cementerio), approximately 2 km west of Puerto Villamil. Fat sleepers may have been introduced much earlier as older local inhabitants reported the fish being present "as long as they can remember." The fish is not known to impact the native biota. Since 2005 fat sleepers have virtually disappeared after the GNPS opened a channel from the lagoon to the sea to increase the salinity in the lagoon (see Tree frog 1 below; Alex Hearn, personal communication CDRS).

Amphibians

Tree frog 1 (*Scinax quinquefasciata*): This frog is thought to have arrived during the 1997–1998 El Niño, and has since been encountered in Puerto Ayora and Puerto Villamil. It has established breeding populations in the lagoons to the west of Puerto Villamil. The frog is a predator of invertebrates and there is concern the frogs will affect the native species in the lagoons. Spraying a caffeine solution on the frogs has been used as a control method and in 2005 the GNPS created a channel from the sea into the lagoon to increase the salinity of the lagoon (Alex Hearn, personal communication CDRS).

Reptiles

Shieldhead gecko (Gonotodes caudiscutatus): The date of arrival for this species is unclear. In 1892, G. Baur collected four geckos from Wreck Bay (Puerto Baquerizo Moreno), which Garman (1892) described as G. collaris and presumed was a native species. However, van Denburgh (1912) visited Puerto Baquerizo Moreno two decades later and did not find the species. He suggested that Baur actually collected his specimens from Guayaquil, where he collected en route to Galápagos, and then mislabeled the locality. Slevin (1935) supported van Denburgh's conclusions. The species was collected again by Wood (1939), also describing it as G. collaris, although Mertens (1963) is usually attributed with the "rediscovery" of the species (Wright 1983a; Hoogmoed 1989). In 1965 (Vanzolini 1965) accurately described the species as G. caudiscutatus and identified it as native to western continental Ecuador. Puerto Baquerizo Moreno appears marginal habitat for this species as it is found at low densities (Wright 1983a; Olmedo and Cayot 1994). However, it has spread into the highlands and is now found in the community of El Progreso, the surrounding farmland, and national park in higher numbers (Hoogmoed 1989; Olmedo and Cayot 1994). Its preference for mesic habitats has allowed it to invade natural areas; this trait also minimizes the risk of it competing with the native geckos (Phyllodactylus darwini and P. leei), which prefer more xeric habitat (Wright 1983a; Hoogmoed 1989; Olmedo and Cayot 1994). However, native lizards are absent from the highlands, so it is unclear what impact it will have on the native insect fauna. G. caudiscutatus was recently reported from Baltra (Jiménez-Uzcátegui et al. 2007), however this record is suspect due the lack of suitable habitat in urban and natural areas.

Mourning gecko (*Lepidodactylus lugubris*): This species was first recorded in Puerto Ayora in the 1970s (Wright 1983b; Altamirano 2002), probably arriving via shipping from Guayaquil (Hoogmoed 1989). It has since spread to Puerto Villamil and Puerto Baquerizo Moreno (Olmedo and Cayot 1994).

Thus far, its habitat requirements appear to have restricted it to artificially humid areas in towns and mangroves (Altamirano 2002). However, the risk of further dispersal throughout the archipelago may be greater due to its parthenogenesis. Competitive interactions of this species with the native *P. galapa-goensis* were studied and it appears the mourning gecko is not affecting the native species (Altamirano 2002).

Peter's leaf-toed gecko (P. reissi): Found only in Puerto Ayora, this species was first recorded in 1975 (Hoogmoed 1989; Olmedo and Cayot 1994). It is presumed to have arrived via shipment of cargo from the port of Guayaquil to the Galápagos. In 1993, P. reissi was still restricted to Puerto Ayora, but by 2000 it had reached the highland town of Bellavista (Olmedo and Cayot 1994; Altamirano 2002). Despite its range expansion, P. reissi appears to be dependent on urban habitat, not having expanded into natural areas (Altamirano 2002). Because P. reissi is much larger than the native geckos, there is concern it will impact the native species (Olmedo and Cayot 1994). In urban habitats, P. reissi does displace the native gecko, P. galapagoensis, though the mechanism is unclear (Altamirano 2002).

Birds

Domestic duck (*Anas* sp. or *Cairina moschata*): Domestic ducks are found on Isabela, San Cristóbal, and Santa Cruz, but the date of introduction is unclear. In 1937, two white "Peking" ducks were taken from San Cristóbal to Santiago and kept in domestication (Conway and Conway 1947). Four months after their introduction to Santiago, they were taken to Floreana where these two individuals were killed by feral dogs within the first year. No wild populations are known.

Guinea fowl (*Numida meleagridis*): Guinea fowl were first recorded in 2005 (Gottdenker et al. 2005), though they were likely introduced earlier. Domestic birds are confirmed on farms on Santa Cruz (DAW, personal observation.) and reported from farms on Floreana, Isabela, and San Cristóbal (Jiménez-Uzcátegui et al. 2007). There are no known wild populations.

Domestic chicken (*Gallus gallus*): Chickens were first reported on Floreana in 1872 (Wolf 1879; in

Baur 1891). At this time they were likely feral, as Wolf describes them "... found on the highest most inaccessible regions..." Six chickens were introduced to Santiago in 1937 where they bred and roamed freely (Conway and Conway 1947). After four months, presumably all of these animals were removed and taken to Floreana. Currently, they are found on all inhabited islands. Prior to 1997, feral populations were known only from Floreana (Hoeck 1984). Feral populations established on Santa Cruz during the 1997-1998 El Niño, presumably aided by the increased vegetation and related insect abundance (Vargas and Bensted-Smith 2000) and are now also found on Isabela, and San Cristóbal (Gottdenker et al. 2005). In 2002, chickens were observed on Baltra near the military personnel housing and appeared to be semi-feral (RBP, personal observation). Thus far, no impacts to the native biota have been documented, but chickens are reservoirs and vectors of avian diseases, and pose a transmission risk to the native avifauna (Phillips et al. 2003; Gottdenker et al. 2005).

Domestic turkey (*Meleagris gallopavo*): A male and female turkey were introduced to Santiago in 1937 (Conway and Conway 1947). After four months, the male was removed and taken to Floreana, but the female and her brood of unknown number were left on Santiago, with both populations presumed to have gone locally extinct. Turkeys are found on farms on Isabela, San Cristóbal and Santa Cruz (Jiménez-Uzcátegui et al. 2007). No wild populations are known.

Cattle egret (Bubulcus ibis): Cattle egrets were first documented in the archipelago in 1964, but unconfirmed sightings begin in 1960 (Lévêque et al. 1966). This species was originally considered native due to their presumed unaided arrival to the islands (Grant and de Vries 1993). However, they have recently been categorized as aliens by the GNPS & CDRS, because their colonization was likely facilitated by the alteration of the habitat from introduced alien grazers (Weber 1972; Telfair 1994). Cattle egrets have been sighted on many outlying islands (Appendix Table 2; Harris 1973) and are capable of reaching all islands, but breeding usually occurs in mangroves at a few specific sites. Daily migrations to and from roosting sites in mangroves are made to feeding sites, primarily to areas of ungulate grazing in the highlands (DAW & RBP, personal observation). Cattle egrets are not documented to have large scale impacts on native wildlife in the Galápagos, but the potential exists (Bryan et al. 2003; Dugger et al. 2005); (McKilligan 1997). In general, cattle egrets have a catholic diet, which includes terrestrial and marine invertebrates, fish, reptiles and rodents (Siegfried 1971; Gassett et al. 2000) and in Hawaii they prey on chicks of native waterbirds, such as black-necked stilts (Himanotpus mexicanus; Stone and Anderson 1988). In the Galápagos, their diet is probably mostly native invertebrates, such as grasshoppers and other orthopterans and small vertebrates, such as lava lizards and geckos, and possibly hatching land iguanas (HLS, personal observation). Although four native Ardeidae (herons and egrets) breed in the Galápagos, there appears to be little niche overlap with cattle egrets, thus direct competition is unlikely. However, of concern is the potential for large scale damage to mangroves from nesting colonies of cattle egrets. They physically destroy branches and leaves (DAW, personal observation) and the increased nitrogen from their excrement may alter the chemistry of the mangroves.

Rock pigeon (Columba livia): Four rock pigeons were brought to Floreana in 1972 or 1973 for the purposes of establishing a loft (Harmon et al. 1987). Subsequently, descendents of these birds were introduced to the three towns of Puerto Ayora, Puerto Baquerizo Moreno, and Puerto Villamil. Sometime in the early 1980s, the owner of the Floreana loft returned to the continental Ecuador and abandoned his birds, which presumably died. In 1985, the total population of rock pigeons in the archipelago numbered around 200 birds, (Harmon et al. 1987). By 2001, the entire population was around 550 birds, despite harvesting and culling by the GNPS and locals (Phillips et al. 2003). By the early 2000s, the species had become established in the highlands of San Cristóbal and Santa Cruz. In Puerto Ayora, rock pigeons were nesting on cliffs bordering the national park. Though no effects on the native fauna from rock pigeons have been documented, rock pigeons likely transmitted Trichomonas gallinae to the endemic Galápagos dove (Harmon et al. 1987). Transmission of additional and more virulent diseases posed a serious threat to avifauna of Galápagos (Phillips et al. 2003). The GNPS and CDRS began a campaign to eradicate rock pigeons from the archipelago in 2001. The campaign began on Santa Cruz and after completion there, moved to San Cristóbal, then Isabela. The eradication was successfully completed in 2006 (Phillips, unpublished data).

Smooth-billed ani (Crotophaga ani): Anis were first reported in 1962 on Isabela, but mistakenly identified as groove-billed anis (C. sulcirostris; Harris 1973), an error which was propagated in the literature for decades (Wiedenfeld 2006). Exactly how anis arrived in the Galápagos is unclear, but being relatively weak fliers they are thought incapable of colonizing the archipelago unassisted (Grant and de Vries 1993). Instead, anis are believed to have been brought to the Galápagos to control ticks on cattle (Harris 1973). Anis are closely associated with livestock and pasture (Grant and de Vries 1993), but following their arrival are now widely distributed on islands in the archipelago (Appendix Table 2). Despite their weak flight capabilities, anis have made extensive over-water flights (up to 88 km) to reach several islands. In the 1980s, they invaded Pinzón and Santa Fé, but were eradicated. During the 1997–1998 El Niño, which produced an increase in vegetation on islands across the archipelago, anis invaded Daphne Major, Española, Marchena, Pinta, Genovesa, Fernandina, Pinzón and Santa Fé (Vargas and Bensted-Smith 2000). Concomitantly, an increase in ani numbers was observed on Santa Cruz and Alcedo Volcano, Isabela. It is likely that during wet years such as El Niños, anis are able to colonize the smaller, drier islands, but disappear from those islands in dry years, as has apparently happened on Gardner-by-Floreana (Wiedenfeld 2005). Anis are a low priority alien species, not having been attributed with any serious impacts to native species, although it is likely that they have some effects on native invertebrates and prey upon native bird nestlings. Regardless, efforts were taken to remove anis from Fernandina and Genovesa in 2000 and 2001. Anis died out on both islands. The results from a eradication efforts on Marchena in 2007 are unclear (Jiménez-Uzcátegui et al. 2007).

Mammals

Feral cat (*Felis silvestris catus*): Cats were introduced to all inhabited islands and established domestic and feral populations (Appendix Table 3). The date of arrival for cats in the Galápagos is not well documented. It may have coincided with that of the first whalers and buccaneers, since cats were often kept on ships to control rodents (Todd 1977). However, it is more likely that cats first arrived in the archipelago during the early settlement period for each island (Hoeck 1984). Cats invaded Venecia, and Las Bayas Grande and Pequeña. The latter two are small, mostly rocky islets about 100 m off the north coast of Floreana. Invasion by cats of these three uninhabited islands was probably unaided by humans. Cats were reported on Santiago (Eckhardt 1972; Laurie 1983), but there is no evidence a population established. Worldwide feral cats have had widespread and serious negative impacts on insular fauna (Courchamp et al. 2003; Nogales et al. 2004). In the Galápagos, feral cats prey on a variety of native species (Konecny 1987) and are suspected of causing population declines or extinctions of several species, such as the marine iguanas (Laurie 1983), land iguanas (Phillips et al. 2005), Galápagos dove (Zenaida galapagoensis), Galápagos snakes (Alsophis biseralis and Antillophis ssp.), and rice rats (Nesoryzomys spp. and Oryzomys galapagoensis; Dexter et al. 2004). Although, evidence for cats impacting these species is compelling, it remains correlative. To date, the only documented population level impact of cats on Galápagos' fauna is on lava lizards (Microlophus spp.), where lizards exposed to cat predation are more wary than those in cat-free areas (Stone et al. 1994). On Venecia, where before being shot, a single cat substantially reduced the resident lava lizard population (HLS, personal observation). Feral cats have been eradicated from Baltra (Phillips et al. 2005). Prior to the campaign on Baltra, little effort had been directed at controlling feral cats in the Galápagos. As with domestic dogs, WildAid, the CDRS, and GNPS have begun implementing sterilization program for cats in the three largest towns.

Feral dog (*Canis lupus familiaris*): Domestic dogs are found in urban and rural areas on all the inhabited islands, including Baltra (Appendix Table 3). Dogs were likely introduced to Floreana and San Cristóbal during the mid-1800s and to Isabela by 1890 (Heller 1903; Slevin 1931). Their first record from Santa Cruz was about 1925 (Kastdalen 1982). In 1937, three dogs were transported to Santiago, but apparently only two, a male and female, survived the voyage (Conway and Conway 1947). Four months later, they were taken to Floreana, where feral dogs were already abundant. In 1978, an individual dog was found on Santa Fé (Keith Christian, University of Australia, Darwin, personal communication), which is isolated from the nearest other dog population on Santa Cruz by 16.7 km. A single dog was also reported on Venecia, a mangrove-covered islet 30 m off the NW coast of Santa Cruz. Dogs could have arrived unaided on Venecia, whereas the individual on Santa Fé was surely marooned by humans. Feral populations established on all inhabited islands, except Baltra. However, the persistence of a feral population may be dependent on the presence of a domestic population. The feral population on Santa Cruz reportedly went extinct in the 1930s (Kastdalen 1982), but by the 1970s feral dogs were again a serious problem. In 1975, farmers eradicated the feral populations on Floreana and San Cristóbal by poisoning and shooting. In the early 1980s, feral dogs numbered between 25 and 70 on Santa Cruz and between 200 to 500 on southern Isabela (Hoeck 1984). Despite the small population sizes, they have an enormous impact on the native fauna. Local populations of land (Conolophus subcristatus) and marine (Amblyrhynchus cristatus) iguanas are quickly devastated when subject to predation by feral dogs (Kruuk 1979). Seabirds are often an important prey item in the diet of feral dogs and at one location 15 dogs killed about 450 Galápagos penguins (Spheniscus mendiculus) annually (Kruuk 1979). On Santiago, dogs are mentioned as affecting land iguanas and tortoises along with pigs (Hoeck 1984, p. 239), but there is no evidence they established a population on Santiago. The feral dog population at Conway Bay on Santa Cruz was eradicated in the early 1980s to protect land iguanas (Cayot et al. 1994), while on southern Isabela, control efforts have reduced feral dogs to extremely low levels. The dog on Santa Fé was removed at the time it was discovered (Keith Christian, University of Australia, Darwin, personal communication), while the one on Venecia either emigrated or died. More recently the non-profit organization WildAid, with support from the GNPS and CDRS, has begun implementing a sterilization program for dogs in the three largest towns.

Feral donkey (*Equus asinus*): Donkeys were first recorded in the Galápagos on Floreana in 1834 (Coulter 1845; in Carrion et al. 2007) and on San Cristóbal in 1847 (Hoeck 1984), being introduced to transport barrels of tortoise oil (Van Denburgh 1914). By the late 1800s, they were also found on Isabela,

Santa Cruz, and Santiago (Cookson 1875; Baur 1891). Donkey populations were described as numerous on these islands, but their relative abundance was considered low, with only a few hundred individuals on Santiago and Volcan Alcedo, Isabela (Carrion et al. 2007). Though relatively low in numbers, donkeys have multi-level impacts on the Galápagos' biota. They potentially compete for food resources with several species, most notably tortoises and land iguanas (Fowler de Neira and Johnson 1985). Donkeys also impact tortoises and land iguanas by trampling their nests (Fowler de Neira and Roe 1984). Their physical activity is suspected of altering the vegetation structure, by removing the understory (Hamann 1984). Giant prickly pear (Opuntia spp.) are particularly susceptible to donkey herbivory, suffering increased mortality through being toppled or girdled or by reduced recruitment (van der Werff 1982; Hicks and Mauchamp 1995). Sporadic control of donkeys on Santiago and Alcedo Volcano has been conducted for decades (Carrion et al. 2007). In 2004, donkeys were eradicated on Santiago and in 2005 from northern Isabela. These eradication efforts were conducted in conjunction with eradication campaigns on goats and pigs (Carrion et al. 2011). Between 2006 and 2009, 380 donkeys were removed from Floreana resulting in their eradication. On the remaining islands where donkeys are present, removal efforts by the GNPS are continuing.

Feral horse (*E. caballus*): Domestic horses are found on all inhabited islands, except Baltra (Appendix Table 3; Hoeck 1984). Feral populations have established only on the volcano Sierra Negra on Isabela. Prior to 2004, locals captured juveniles occasionally for domestication. After 2004, locals made a concerted effort to capture all horses and since 2006 no feral horses have been seen on Sierra Negra.

Feral pig (*Sus scrofa*): Pigs were first introduced to Floreana in 1832, San Cristóbal in 1847, southern Isabela in 1897, Santa Cruz in the 1920s, and Santiago before 1930 (Hoeck 1984). Because pigs are omnivores they can have wide-ranging impacts on the native biota of Galápagos. As predators, pigs prey on the eggs and hatchlings of sea turtles (*Chelonia mydas*) and tortoises (MacFarland et al. 1974; Green 1979; in Coblentz and Baber 1987). On Santiago, pigs were a probable factor in the extinction of land iguanas (Coblentz and Baber 1987). They root for and eat the roots, rhizomes, and tubers of many native plants, having decreased the distribution of two orchid species (Hamann 1981; Kastdalen 1982; van der Werff 1982). Pigs may also spread invasive plants by consuming and dispersing their seeds (e.g. guava; Coblentz and Baber 1987). Pigs were long recognized as a threat to the Galápagos' flora and fauna. Efforts to control them on Santiago, albeit limited and sporadic, began in 1968 (Cruz et al. 2005). Their eradication from Santiago was planned at a symposium in 1982. In 1982 and 1983, research was conducted on Santiago to understand pig population dynamics and develop strategies for their eradication (Coblentz and Baber 1987). Control efforts increased in the mid-1970s and persisted through 2000, with the last pig on Santiago being detected in October 2000 (Cruz et al. 2005). Aside from the eradication program on Santiago no systematic efforts have been directed at controlling pigs.

Feral cattle (Bos taurus): Cattle first arrived on Floreana in 1832 (Hoeck 1984), San Cristóbal in 1847, southern Isabela after 1890 (Koford 1966), and Santa Cruz after 1923 (Kastdalen 1982). Feral populations established quickly and eventually occurred on all four islands (Hoeck 1984). Feral cattle were reported to number 10,000-30,000 on southern Isabela's Cerro Azul volcano. On Sierra Negra, self-sustaining herds of domestic and semiferal cattle provide income to local inhabitants. The impacts of feral cattle are particularly evident in the Miconia and Fern-Sedge Zones (see review in Schofield 1989). Cattle grazing and trampling in the Fern-Sedge Zone on Isabela created open areas allowing alien grasses to invade and on San Cristóbal their activities altered the structure of the Miconia Zone amd diminished stream-flow from a crater lake. On San Cristóbal cattle trampling has caused the collapse and destruction of Galápagos petrel nest burrows (Cruz-Delgado et al. 2010). They also aid in the spread of guava (Psidium guajava), an extremely invasive tree, by first creating open areas and spreading the seeds in their feces (van der Werff 1979; de Vries and Black 1983; Schultz 2003). During the 1970s and 1980s, hunting by locals and culling by GNPS reduced feral populations on all islands. In 2008, feral cattle were eradicated on Floreana in conjunction with a feral goat and donkey eradication campaign. In early 2011, control efforts on San Cristóbal greatly reduced feral cattle numbers. An unknown number of feral cattle remain on Isabela and San Cristóbal.

Feral goat (*Capra hircus*): Goats were first confirmed on Santiago in 1813, but are reported introduced there in the 1600s (Hoeck 1984). No records exist for their introduction to Floreana, San Cristóbal, Isabela, and Santa Cruz, but they likely arrived when humans were settling each island. In 1905, goats were also present on Baltra, Santa Fé, and Española (Slevin 1931). They were introduced to Pinta in 1959, to Marchena in 1967 and to Rábida in 1971 (Hoeck 1984). Five goats were also briefly introduced to Plaza Sur, in the 1960s (Craig MacFarland 1977, Colorado State University, personal communication). In 1990, five goats were discovered on tiny (1.3 ha) Marielas Sur (Carrion et al. 2011). In 2009, one goat was discovered on Wolf (Atkinson et al. 2011). The impact of goats on Galápagos' biota is well documented (Hamann 1984; Schofield 1989). High population densities and intense browsing and grazing denude the landscape of most vegetation. Regeneration of woody species is prevented due to browsing of seedlings. This transforms previously dense stands of vegetation into open parklands with even-aged trees and shrubs. The altered landscape facilitates invasion of alien plants. In turn, native animals such as tortoises are affected because the degraded habitat is less productive and supports fewer individuals. Goats now remain on only three islands, having been eradicated from all of the above islands except Santa Cruz, San Cristóbal, and Southern Isabela. (Appendix Table 3; Carrion et al. 2011). Eradication efforts are underway on the latter two islands and population reduction on the former, in part to minimize the threat of intentional reintroductions to islands previously cleared of goats (Carrion et al. 2011).

Domestic sheep (Ovis aries): Feral sheep do not occur in the Galápagos, but domestic sheep were found on farms on Santa Cruz, and possibly San Cristóbal and Isabela into the 1970s. In 1962, sheep were released on Sierra Negra, southern Isabela, but did not establish a feral population (Duffy 1981). Hoeck (1984) suggested sheep were unlikely to pose a threat to the flora and fauna of Galápagos because feral populations would only thrive in cold climates (Holdgate 1967). Fortunately for the Galápagos, this theory was not tested. Feral sheep are found Socorro Island, Revillagigedos, Mexico on

(18°N; Walter and Levin 2008) and at one time were found on several of the Channel Islands, California, USA (33° N; Jorgensen and Ferguson 1984; Klinger et al. 2002). In the above archipelagos, feral sheep grazing severely degraded the habitat.

House mouse (Mus musculus): House mice were first recorded on San Cristóbal in 1899 (Snodgrass and Heller 1899) and Floreana and Santiago in 1906 (Hunter 1906). However, their invasion to the archipelago likely occurred much earlier, coinciding with the arrival of whalers and small-scale settlement on Santiago in the 1600s. On Santa Cruz, house mice were first reported in the 1940s (Kastdalen 1982) and are now found on all islands which have or had human inhabitants. During an El Niño event in 1982-1983, house mice invaded Plaza Norte and Plaza Sur (Calvopia 1986; Snell et al. 1994). In 1989, house mice were reported on Seymour Norte and Mosquera (Key and Muñoz Heredia 1994), however on subsequent surveys they were not detected, either going locally extinct or perhaps being extirpated by black rats. In 1984, Hoeck (1984) reported house mice occurred on six islands. Ten years later, 10 islands were reported to have been invaded (Key and Muñoz Heredia 1994). Currently, we document mice present on eight islands (Appendix Table 3). House mice are a pest in and around human habitation, but to date they have had little impact on native species in the Galápagos. Snell et al. (1994) suggest house mice may accelerate Opuntia sp. mortality and recent research on Gough Island indicates house mice contribute significantly to seabird mortality (Wanless et al. 2007). In January 2011, rodenticide was applied to Plaza Norte, with results pending.

Norway rat (*Rattus norvegicus*): This species likely arrived via cargo ships from Guayaquil, Ecuador (Cody Edwards, George Mason University, personal communication). It was first reported on Santa Cruz in 1983 or 1984 (Fielder 1984) and about four years later arrived on San Cristóbal (Sivinta-Mena 1988). By 1988, they were found in association with habitations in the small community of Bellavista on Santa Cruz. In the 10 years from its arrival, the population of Norway rats expanded from Puerto Ayora into several locations in the central highlands, including the agricultural zone and Los Gemelos in the *Scalesia* zone (Key and Muñoz Heredia 1994;

Key et al. 1994). By 2000, Norway rats were found in the western highlands in the Scalesia zone along the road to Garrapatero. As of 2002, on Santa Cruz, Norway rats were the dominant rodent in urban zones, but black rats still outnumbered them away from human habitation. We confirmed Norway rats were still present on San Cristóbal, but had not yet arrived on Floreana or Isabela. Their only other occurrence in the archipelago is on Rábida, where they were detected in 2004 (Dexter et al. 2004). Their arrival on Rábida was presumably aided by boat traffic from either Puerto Ayora or Puerto Baquerizo Moreno. Norway rats were reported to occur on Santiago before 1900 (Atkinson 1985) based on a record from the California Academy of Sciences 1899 expedition. A subsequent examination of this specimen revealed it to be a black rat (Moe Flannery, California Academy of Sciences, personal communication). Aside from their role as a human and agricultural pest, Norway rats have not been associated with any impacts to the Galápagos biota. However, if their range expands to other islands, either via boats or by further colonization of Santa Cruz, which would put them in swimming range of several offshore islands (Atkinson 1985; Russell et al. 2005), then serious impacts to Galápagos' fauna would be predicted. Though Norway and black rats have similar ecological impacts, Norway rats are larger, more aggressive, and have greater impacts on large seabirds (250-750 g; Holdaway 1999). In January 2011, rodenticide was applied to Rábida, with results pending.

Black rat (R. rattus): Darwin was the first to document black rats in the Galápagos in 1835 on Santiago (Patton et al. 1975). However, their introduction to the archipelago is thought to have occurred during the 1600s with arrival of whalers and buccaneers. Genetic and morphometric analyses indicate that the introduction in the 1600s was the first of three or four periods (Patton et al. 1975). The second period of introduction is thought to have occurred on Floreana in the mid-1800s, and from there black rats were transported to Isabela and San Cristóbal during the mid-to late 1800s. The third period of introduction was to Santa Cruz in the 1930s, and to Baltra shortly thereafter when the U.S. occupied the island during World War II. Pinzón, invaded in the 1800s, may represent a fourth invasion to the archipelago or an inter-archipelago movement of rats from the Floreana-Isabela-San Cristóbal group. Hoeck (1984) reported eight islands with black rats in 1984 and Key and Muñoz Heredia (1994) reported black rat as present on 10 islands total. Our work reveals black rats have invaded at least 36 islands, including three of the five islands in the brackish lake on Isabela; however, some populations have been eradicated (Appendix Table 3).

Though the overall impact is serious, the number of native species directly documented as impacted by black rats is small. On Pinzón, recruitment of juvenile Galápagos tortoises (*Geochelone ephippium*) into the population is almost zero due to black rats preying on hatchlings (MacFarland et al. 1974). Black rats also prey heavily on the eggs and nestlings of the Galápagos petrel (*Pterodroma phaeopygia*) contributing to their decline (Cruz and Cruz 1987; Cruz-Delgado et al. 2010). Circumstantial evidence suggests black rats were a factor in the extinction of several species of native Galápagos rodents (reviewed in Clark 1984); however, feral cats may have played a role in the extinction of native rodents (Dexter et al. 2004).

Hoeck (1984) suggested black rats could not be eradicated, nor controlled in the Galápagos. Black rats have proven difficult to control in the petrel nesting colonies, hindering the bird's recovery, and there have been some notable failed eradication attempts (e.g. Pinzón, 1815 ha; Appendix Table 3). However, Hoeck's prediction is fortunately proving inaccurate. On Bartolomé (124.5 ha), a campaign of poisoning and trapping in 1976 likely resulted in the eradication of black rats, though they are again abundant on the island, apparently having either recolonized from nearby Santiago or arrived via boat. Recently, successful eradications have been conducted on several islands ranging in size from 0.07 to 183.9 ha, with one failed attempt on Bainbridge 1 (1.4 ha).

Account of species that failed to establish

Amphibians

Marine toad (*Chaunus (Bufo) marinus*): Reported from San Cristóbal in 1995 (CDRS internal records).

Tree frog 2 (*Eleutherodactylus unistrigatus*): Reported from Isabela (CDRS internal records).

Tree frog 3 (*Hyla* sp.): Reported from San Cristóbal in 1990 (CDRS internal records).

Reptiles

Yellow-footed tortoise (*Geochelone denticulata*): Reported from Santa Cruz (CDRS internal records).

Common slider turtle (*Trachemys scripta*): A single turtle was intercepted and dispatched in 2006. The locality is uncertain, but was reported as Santa Cruz.

Yellow-spotted river tortoise (*Podocnemis unifilis*): A single tortoise was intercepted on San Cristóbal in 2006 (Jiménez-Uzcátegui et al. 2007). The animal was killed.

Green iguana (*Iguana iguana*): Locals reported seeing green iguanas on the north coast of Santa Cruz in 1982. In 2000, a green iguana was captured in Puerto Ayora and deposited in the CDRS museum. In 2006, a green iguana was found in Puerto Baquerizo Moreno and removed by GNPS (Jiménez-Uzcátegui et al. 2007).

San Cristóbal leaf-toed gecko (*Phyllodactylus leei*): This species is endemic to San Cristóbal, but was found in Puerto Villamil (Wood 1939). There have been no further reports of this species on Isabela, or elsewhere outside its natural range (Olmedo and Cayot 1994).

Leaf-toed gecko (P. tuberculosus): The presence of this species in the Galápagos is doubtful. A native of Central America, P. tuberculosus was reported in Galápagos on three California Academy of Sciences (CAS) expeditions dating from 1887 to 1906 (Van Denburgh 1912). Van Denburgh (1912) reports collecting 21 specimens of P. tuberculosus from San Cristóbal on CAS expeditions from 1905–1906. Subsequently, no additional specimens were collected (Vanzolini 1965; Olmedo and Cayot 1994). Taylor (1942) reexamined the CAS specimens and identified them as P. darwini, a San Cristóbal endemic. Unfortunately, confusion regarding the status of P. tuberculosus in the Galápagos persists. In an essay on the threat of "insidious" invaders, Lundh (1998) mentions this species again as an alien on San Cristóbal and the Charles Darwin Foundation recently listed this species as one of three introduced geckos (CDF 2010). To further confuse the species' status, two recent guide books on the Galápagos list *P. tuberculosus* as a resident native species on San Cristóbal (Fitter et al. 2000; Swash and Still 2000). It now seems certain *P. tuberculosus* never occurred in the Galápagos, and the purported specimens were *P. darwini*. This species is not listed in Appendix Table 1.

Five-lined skink (*Eumeces inexpectatus*): A single gravid lizard was found on San Cristóbal and dispatched (Jiménez-Uzcátegui et al. 2007).

Birds

Domestic goose (*Anser anser*): Geese are reported from San Cristóbal, but the date of introduction is unknown (Jiménez-Uzcátegui et al. 2007).

Asian quail (*Coturnix* sp.): Quail were first reported in 2001 and from Floreana, Isabela, Santa Cruz, and San Cristóbal (Jiménez-Uzcátegui et al. 2007).

Green peafowl (*Pavo muticus*): Peafowl were reported in 2006 or 2007 from San Cristóbal (Jiménez-Uzcátegui et al. 2007).

Red-masked parakeet (*Aratinga erythrogenys*): In April 1996, locals reported two to three feral parakeets on San Cristóbal flying between Puerto Baquerizo Moreno and the National Park (Vargas 1996). Later that month, a single bird was observed and identified near Puerto Baquerizo Moreno. The species did not establish and apparently died out (Wiedenfeld 2006).

Great-tailed grackle (*Quiscalus mexicanus*): In 2010, a single grackle was intercepted in Puerto Ayora and removed (Jiménez-Uzcátegui, Charles Darwin Research Station, personal communication).

Mammals

Monkey: Three individuals of an unidentified species of monkey (Appendix Table 3) were reported from Floreana in the 1930s (Duffy 1981). They all died of unspecified causes. In 2006, a pet cotton-top tamarin (*Saguinus oedipus*) was discovered on a private boat at San Cristóbal. Ocelot (*Leopardus pardalis*): Two ocelots were brought to Santiago in 1937 for the purpose of breeding and selling the offspring as "tigers" to yachtsmen traveling to the island (Conway and Conway 1947). Approximately 3 months after being introduced to the island the Governor of the Galápagos ordered the ocelots killed since, "it was against the law to import beasts of prey to the Galápagos, lest they escape to stock the islands and kill off the useful animals." (Unfortunately, such wisdom has not been universally applied!). Instead, the owner was allowed to leave and take the animals back to the mainland.

Deer: In 1966, a male and female of an unnamed species were introduced to San Cristóbal (Duffy 1981). No population established.

Guinea pig (*Cavia porcellus*): In 1937, two guinea pigs were brought to Santiago, but their owner left a few months later and the fate of the animals is unknown (Conway and Conway 1947). In 1965, CDRS records report free-roaming guinea pigs in households in the highlands of San Cristóbal and Santa Cruz (Duffy 1981). Hoeck (1984) also reported guinea pigs were kept on farms on Santa Cruz, and suggested they may have been kept on Isabela and San Cristóbal. Jiménez-Uzcátegui et al. (2007) reported guinea pigs may be present on Floreana. It currently appears no feral populations have established, possibly due to their inability to survive without human support (Duffy 1981). The present status of guinea pigs is unclear.

European rabbit (*Oryctolagus cuniculus*): Rabbits are reported from San Cristóbal and Santa Cruz (Jiménez-Uzcátegui et al. 2007). A small colony was reported in the "pampas" of San Cristóbal in 1965, but it apparently went extinct (Duffy 1981). As of 2001, a single owner on San Cristóbal had dozens of rabbits in captivity and was ordered to remove them, but their present status is unclear. Fortunately, rabbits have not established feral populations. Introductions of rabbits frequently succeed (Flux and Fullagar 1992) and they can have impacts on multiple levels as herbivores and as prey items for other introduced species (Courchamp et al. 2003).

Discussion

Our review represents the first comprehensive examination of the history, distribution, and impact of alien vertebrates in the Galápagos Islands. In 1984, 13 species of alien vertebrate were reported in the Galápagos (Hoeck 1984). Twenty seven years later, 44 alien vertebrates have been reported. This increase in number of species is not entirely due to new invasions. Some aliens, such as smooth-billed anis were simply omitted, while the status of other species was at the time unclear. In the early 1980s, cattle egrets were considered native and the status of alien geckos was still being resolved (Wright 1983a, b). However, the increase in alien vertebrates from 1984 to 2011 was in part due to at least seven new invasions, including Norway rats and tilapia.

As with the introduction of alien plants and invertebrates, alien vertebrates have altered the unique native vertebrate community of the Galápagos. This is happening partially through extinction (e.g. loss of three of the seven native rice rats; Clark 1984; Dowler et al. 2000) and through homogenization (Lockwood et al. 2000). Alien mammals now outnumber extant native mammals by almost two to one. And two new categories of vertebrates, amphibians and freshwater fishes, occur in the archipelago. Surprisingly, the most diverse native vertebrates, reptiles and birds, are the least affected. Alien birds represent a small percentage of the total avifauna and neither alien reptiles nor birds have had serious impacts on the native biota.

Some species of alien vertebrate are clearly a greater threat to the Galápagos. Feral goats, pigs, and donkeys have proven extremely destructive, but the GNPS has demonstrated its ability to eradicate these animals on a very large scale (Cruz et al. 2005; Carrion et al. 2007). Others, such as rock doves appear confined to a restricted habitat and have proven logistically easier to eradicate.

The future of new vertebrate invasions to the Galápagos appears to be shifting away from the intentional introduction of large species (e.g. goats and chickens) toward hitchhiking cryptic species (e.g. frogs), pets and novelty species (e.g. monkeys and iguanas). The vertebrates posing the greatest threat to the Galápagos may be reptiles (e.g. lizards and snakes). Small species and juveniles are difficult to detect in cargo, individuals can survive extended periods en route, and in contrast to amphibians and fish, the entire archipelago is potentially suitable habitat. Moreover, some species of reptile, such as the common house gecko (*Hemidactylus frenatus*)

and the brown tree snake (*Boiga irregularis*), have demonstrated impacts as insidious invaders (Savidge 1987; Case et al. 1994; Cole et al. 2005; Rodda and Savidge 2007). Reducing the threat posed by alien vertebrates to the Galápagos will require continuing eradication efforts, maintaining a stringent quarantine program, and thorough understanding of their distribution and impacts.

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Appendix

See Tables 1, 2, and 3.

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Name	Size (ha)	ORNI	DOLA	Size (ha) ORNI DOLA CHMA ELUN HY sp. SCQU GEDE TRSC POUN IGIG GOCA LELU PHLE PHRE EUIN	ELUN	HY sp.	scqu	GEDE	TRSC	POUN	IGIG	GOCA	LELU	PHLE	PHRE	EUIN
Isabela	458812		z		R		z						N	Е		
Santa Cruz	98555						z	R	I		R		z		z	
San Cristóbal	55809	Х		R		R	R			I	I	z	z			I
Baltra	2619.6											R				
Species code: ORNI (Oreochromis niloticus); DOLA (Dormitator latifrons); CHMA (Chaunus marinus); ELUN (Eleutherodactylus unistrigatus); HY sp. (Hyla sp.); SCQU (Scinax quinquefasciata); GEDE (Geochelone denticulata); TRSC (Trachemys scripta); POUN (Podocnemis unifilis); IGIG (Iguana iguana); GOCA (Gonotodes caudiscutatus): LELU (Lepidodactylus lugubris); PHLE (Phyllodactylus leei); PHRE (P. reissi); EUIN (Eumeces inexpectatus)	ORNI (Oreo efasciata); G dactylus lugu	chromis n EDE (Geu ubris); PH	iiloticus);] ochelone d LE (Phylld	DOLA (Do [enticulata)] odactylus la	rmitator la ; TRSC (T eei); PHRI	atifrons); (rachemys : E (P. reiss	CHMA (C scripta); P(i); EUIN (haunus mc JUN (Pod Eumeces i	urinus); E ocnemis u nexpectati	LUN (Eler inifilis); IG us)	utherodae IIG (Igua	ctylus unis na iguana	trigatus);); GOCA	HY sp. ((Gonotode	Hyla sp.); es caudisci	SCQU <i>utatus</i>);

islands in the Galápagos archipelago

amphibian, and reptile species and their status on

able 1 List of alien fish,

Amphibian

Fish

Island

Reptile

ΖI

 \Box

Presence codes: E extinct, I intercepted, N naturalized, R reported, X eradicated

Island		Bird											
Name	Size (ha)	ANAN	DUCK	NUME	CO sp.	PAMU	GAGA	MEGA	BUIB	COLI	ARER	CRAN	QUME
Isabela	458812		D	R	R		Ν	D	N	Х		Ν	
Santa Cruz	98555		D	D	R		Ν	D	Ν	Х		Ν	Ι
Fernandina	64248								0			0	
Santiago	58465		Н				Н	Н	Ν			Ν	
San Cristóbal	55809	R	D	R	R	R	Ν	D	Ν	Х	Е	Ν	
Floreana	17253		Н	R	R		Ν	Н	Ν	Е		Ν	
Marchena	12996								0			N*	
Española	6048.0								0			0	
Pinta	5940.0								0			0	
Baltra	2619.6						D		0			Ν	
Santa Fé	2413.0								0			Ν	
Pinzón	1815.0								0			Ν	
Genovesa	1410.8								0			0	
Rábida	499.31								0			0	
Seymour Norte	183.89											0	
Gardner por Floreana	81.17											0	
Gardner por Española	58.04											0	
Daphne Major	33.02											0	
Eden	23.02											0	
Venecia	13.28								0				
Tintorera (I)	12.43								0				
Daphne Chica	7.96											0	
Punta Bowditch Norte	2.92								0				
Villamil Sureste (J)	2.81								0				
Punta Bowditch Sur	1.51								0				
Fondiadero (H)	1.18								0				
Muelle (K)	0.59								0				
de Canal Sur	0.35								0				
Punta Bowditch Este	0.35								0				
Devine	0.30								0				
Faro (G)	0.30								0				

Table 2 List of alien bird species and their status on islands in the Galápagos archipelago

Species code: ANAN (Anser anser); DUCK (Anas sp. or Cairina moschata); NUME (Numida meleagridis); CO sp. (Coturnix sp.); PAMU (Pavo muticus); GAGA (Gallus gallus); MEGA (Meleagris gallopavo); BUIB (Bubulcus ibis); COLI (Columba livia); ARER (Aratinga erythrogenys); CRAN (Crotophaga ani); QUME (Quiscalus mexicanus)

Presence codes: *D* domesticated, *E* extinct, *H* historical record, *I* intercepted, *N* naturalized, *O* occasional (individuals persisting for days to weeks); *R* reported, *X* eradicated. * Eradication campaign underway at time of publication

ISIAIIU		Maillia	_															
Name	Size (ha)	MONK	SAOE	FESI	LEPA	CALU	J EQAS	EQCA	SUSC	DEER	BOTA	CAHI	OVAR	MUMU	RANO	RARA	CAPO	ORCU
Isabela	458812			z		z	z	D	z		z	*z	Н	Z		z	ы	
Santa Cruz	98555			z		z	z	D	z		D	z	Η	z	z	z	R	ч
Santiago	58465			Η	Η	Η	х		Х			x		z		z	Η	
San Cristóbal	55809		I	z		z	z	D	z	Н	z	\mathbf{z}^{*}	Η	z	z	z	R	ч
Floreana	17253	Щ		z		z	х	D	z		D	x		z		z	R	
Marchena	12996											Х						
Española	6048.0											Х						
Pinta	5940.0											х						
Baltra	2619.6			Х		D						Х		z		z		
Santa Fé	2413.0					х						x						
Pinzón	1815.0															z		
Rábida	499.31											x			\mathbf{x}^{*}			
Seymour Norte	183.89													Щ		х		
Wolf	134.40											x						
Bartolomé	124.48															*z		
Cuatro Hermanos #2	30.41													n	n	n		
Eden	23.02															z		
Sombrero Chino	20.88															*z		
Cuatro Hermanos O.	20.42													n	n	n		
Bainbridge #3	18.34															\mathbf{z}^{*}		
Venecia	13.28			Х		Щ										z		
Tintorera (I)	12.43															z		
Plaza Sur	11.90											x		z				
Bainbridge #1	11.42															*z		
Plaza Norte	8.84													\mathbf{z}^{*}				
Cuatro Hermanos E.	7.26													n	Ŋ	Ŋ		
Lobos	6.67															z		
Leon Dormido	5.02													Ŋ	Ŋ	Ŋ		
Mosquera	4.63													Э		x		
Redonda	4.31													Ŋ	Ŋ	Ŋ		
Cowley	3.50													U	Ŋ	Ŋ		
Bainbridge #4	3.44															×		
Watson	3.05													D	D	Ŋ		
Dunta Bowditch Norte																		

Name		TATALLITAL																
1 and	Size (ha)	MONK	SAOE	FESI	LEPA	CALU	EQAS	EQCA	SUSC	DEER	BOTA	CAHI	OVAR	MUMU	RANO	RARA	CAPO	ORCU
Gordon Este	2.91													U	U	U		
Bainbridge #2	2.90															z		
Villamil Sureste (J)	2.81															z		
La Loberia	2.37													n	D	n		
Las Bayas Grande	2.07			х														
Cráter Beagle #2	1.70															z		
Cráter Beagle #1	1.56															z		
Punta Bowditch Sur	1.51															z		
Marielas Sur	1.25											x				x		
Fondiadero (H)	1.18															z		
Leon Dormido P.	0.98													n	n	n		
Gordon Oeste	0.83													U	Ŋ	Ŋ		
Dalrymple	0.80													n	D	n		
Este	0.74													D	D	n		
Viuda	0.68													n	D	Ŋ		
Cráter Cerro Azul	0.60													U		U		
Muelle (K)	0.59															z		
Pitt (nearshore)	0.50													U	D	Ŋ		
Pitt (offshore)	0.40															x		
Espejo	0.36													n	D	Ŋ		
de Canal Sur	0.35													n	D	n		
Punta Bowditch Este	0.35															z		
Blanca	0.30													U	Ŋ	Ŋ		
Faro (G)	0.30													n	D	n		
La Botella	0.27													D	D	n		
Gordon Central	0.26													n	D	n		
Marielas Norte	0.24															x		
Logie	0.20															Х		
El Arco	0.20													n	D	Ŋ		
Las Bayas Pequeña	0.15			x														
Caleta Tiburon Norte	0.14													U	D	Ŋ		
Caleta Tiburón Sur	0.10															z		
El Torre	0.10													U	D	D		
La Ventana	0.10													U	Ŋ	U		

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Island		Mammal									
Name	Size (ha)	MONK	SAOE	FESI	LEPA	CALU	EQAS	MONK SAOE FESI LEPA CALU EQAS EQCA SUSC DEER BOTA	SUSC	DEER	BOT/
Cráter Beagle #5	0.10										
Noroeste de Santa Fe	0.07										
Marielas Este	0.07										
Onan	0.06										
Union	0.05										
El Trompo	0.04										
Rata	0.04										
Ballena	0.01										

Species code: MONK (Monkey sp.); SAOE (Saguinus oedipus); FECA (Felis silvestris catus); LEPA (Leopardus pardalis); CALU (Canis lupus familiaris); EQAS (Equus asinus); EQCA (E. caballus); SUSC (Sus scrofo); DEER (Deer sp.); BOTA (Bos taurus); CAHI (Capra hircus); OVAR (Ovis aries); MUMU (Mus musculus); RANO (Rattus norvegicus); RARA (R. rattus); CAPO (Cavia porcellus) Presence codes: D domesticated, E extinct, H historical record, I intercepted, N naturalized, R reported, U unknown, X eradicated. * Eradication campaign underway at time of publication **ORCU** (Oryctolagus cuniculus)

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