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Biogeography of alien vertebrates in the Galapagos Islands : patterns, processes, and conservation implications

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BIOGEOGRAPHY OF ALIEN VERTEBRATES IN THE GALAPAGOS ISLANDS: PATTERNS, PROCESSES, AND CONSERVATION IMPLICATIONS

BY

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B.A., Biology, University of Northern Colorado, 1987
M.Sc., Ecology, Utah State University, 1999

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy
Biology

The University of New Mexico
Albuquerque, New Mexico

December, 2010

DEDICATION

In memory of my mother, Evelyn “Pat” Starrak, and father, Jerry Phillips, neither of whom made it to see this milestone.

This dissertation is dedicated to my wife, Holly Phillips, whose support and encouragement in this endeavor has never flagged, and whose belief in me has helped me attain my greatest academic goal.

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I am indebted to Howard Snell. At various times he has been my boss, advisor, and mentor, and in each role he has provided the right amount of support, patience, cajoling, or criticism. I will be forever thankful to him for his help in attaining this goal and for providing the opportunity to work in the Galápagos Islands, a dream of most biologists.

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And finally thanks to the Galápagos Islands, may you survive us.

BIOGEOGRAPHY OF ALIEN VERTEBRATES IN THE GALÁPAGOS ISLANDS: PATTERNS, PROCESSES, AND CONSERVATION IMPLICATIONS

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ABSTRACT

Alien species are one of the principal threats to global biodiversity. Insular ecosystems have proven exceptionally susceptible to invasion by aliens and vulnerable to their negative effects. Some of the most destructive alien species are vertebrates, in part due to their having been introduced to islands worldwide. Rodents (*Rattus* spp. and *Mus musculus*) are among the most widespread and devastating invasive species for insular flora and fauna.

In this research I investigate the biogeographic patterns and processes of alien vertebrates in the Galápagos Islands, focusing on the mechanisms that influence their dispersal and colonization within the archipelago. In the first study, I review and synthesize the available literature on alien vertebrates in the Galápagos. I investigate the impacts to the native flora and fauna from alien vertebrates and the spatial and temporal patterns of colonization in the archipelago. I summarize management efforts directed at alien vertebrates and assess the potential future impacts to the Galápagos from alien vertebrates. In the second study, I examine the distribution of the three alien rodents from a biogeographic perspective. Island area and isolation from a source population are examined to determine the influence of these landscape features on the incidence of a rodent species on an island. In the third study, I conduct a multivariate analysis of the biotic and abiotic factors influencing intra-archipelago dispersal and colonization of two alien rodents. Using this analysis the probability of an alien rodent occurring on an island is determined and the risk of invasion to other islands is estimated.

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CHAPTER 1

CURRENT STATUS OF ALIEN VERTEBRATES IN THE GALÁPAGOS ISLANDS: THEIR DISTRIBUTION, ECOLOGICAL IMPACTS AND TAXONOMIC TRENDS

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ABSTRACT

Alien species from each of the five Classes of vertebrates have invaded the Galápagos Islands. We reviewed the current distribution alien vertebrates in the archipelago, their impacts on native species, management efforts aimed at alien vertebrates, and the spatial and temporal trends of the colonization dynamics of alien species. A total of 43 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 the decline or extinction of several species. To date, no other Class of alien vertebrate has had documented impacts on native species. Large and medium-sized mammals and birds have been successfully eradicated from several islands. Invasion patterns appear to be shifting from introductions of livestock species to

accidental arrivals of cryptic species and intentional introductions of pet species, illustrating the need to strengthen and maintain quarantine programs.

INTRODUCTION

Alien species are now widely recognized as one of the principal threats to global biodiversity (Vitousek *et al.*, 1997). 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). As managers better understand the threat posed by alien species to insular native flora and fauna, efforts are increasingly directed towards eradicating aliens (Myers *et al.*, 2000; Simberloff, 2001; Veitch & Clout, 2002). Successful eradication campaigns usually require a large logistical effort, great financial resources, and assurance that the risk of reinvasion is minimal (Myers *et al.*, 2000). Therefore, it is critical to identify and understand the processes and pathways of alien invasion, and for archipelagos the mechanisms of inter-island movement (Wittenberg & Cock, 2001; Christy *et al.*, 2007).

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 Galápagos have experienced proportionately fewer extinctions and ecosystem disruptions compared to islands with longer human occupation (e.g. the Hawaiian Islands). Despite the relatively brief human occupation, hundreds of alien species, representing a wide variety of taxa, have invaded the archipelago. 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 & Snell, 1981; Hamann, 1984; Cruz & Cruz, 1987). Of the IUCN's 100 worst invasive alien species, 29 are vertebrates, and seven of these have been reported in the Galápagos (Lowe *et al.*, 2000).

Numerous authors have reported on the presence and impact of alien vertebrates in the Galápagos (Eckhardt, 1972; de Vries & Black, 1983; Laurie, 1983; Hoeck, 1984) Hoeck's (1984) review, the most thorough, provided a fairly accurate summary of the conditions a quarter century ago. Since then, human migration from the Ecuadorian continent has increased greatly as has the human population. The growth of the population has resulted in an increase in the shipping of goods to the archipelago from the Ecuadorian continent, thus increasing the avenues of invasion for aliens. In conjunction with a burgeoning population there has been a growth in tourism and industry (e.g. fishing), which has resulted in an increase in movement between islands. 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 three objectives: 1) synthesize the available information on alien vertebrates in the Galápagos and provide a current review of the number and distribution of species in the archipelago; 2) assess the impact of alien vertebrates on the native biota; and 3) examine introductions from a temporal and spatial perspective to determine if trends or patterns are apparent. Our work should provide biologists and managers information to help prioritize and direct management of alien species within the Galápagos, and elsewhere.

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 to 40,000 (UNESCO, 2010) is dispersed across five islands: Santa Cruz, San Cristóbal, Floreana, Isabela, and Baltra (Fig. 1). Baltra is not part of the national park and is administered by the Ecuadorian Air Force, the Ecuadorian Navy, and the Municipality of Santa Cruz. The majority of the population lives on Santa Cruz (~24,000), San Cristóbal (~10,000), and Isabela (~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 Galápagos National Park Service. 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. Both of these organizations began operations in the mid-1960s, although their charters date from 1959.

The native vertebrate fauna of the Galápagos is comprised of three taxa: reptiles, birds, and mammals. 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, 3 iguanas) in the Galápagos, excluding sea turtles (Ernst & Barbour, 1989; Thomas, 1997; Swash & Still, 2000). Birds are the largest and most diverse native group, comprised of 68 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 (Dowler *et al.*, 2000; McCracken *et al.*, 1997).

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 & GNP trip reports). Additional data are derived from the authors' previously unpublished research and observations. The authors have a combined 20 yrs 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 GNP 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 GNP or CDRS personnel.

RESULTS

As of 2009, 43 species of alien vertebrate have been reported from Galápagos (Appendices A, B, and C), 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 11, 9, and 4 species, respectively. Only two species of fish have been documented. Of the total species reported, 20 established feral populations. Mammals are the most numerous group of alien vertebrates to establish, with 10 species. Birds and reptiles have four and three species, respectively. One species of amphibian and two species fish have invaded and established populations.

All of the 123 islands have at least 1 alien vertebrate reported (Appendix B), due to the vagility of cattle egrets (*Bubulcus ibis*) and to a lesser extent smooth-billed anis (*Crotophaga ani*). Black rats (*Rattus rattus*) and feral goats (*Capra hircus*) are fairly widespread, having invaded 36 and 13 islands, respectively. Only islands with human inhabitants (past or present) have more than 5 alien species per island: San Cristóbal, 30;

Santa Cruz, 25; Isabela, 21; Floreana, 16; Santiago, 14; and Baltra, 8. Excluding cattle egrets and smooth-billed anis, alien vertebrates have not reached 48 islands. For 30 islands the status of some alien vertebrates is unknown; some species, such black rats may occur on these islands, but surveys have not been conducted.

Alien mammals and birds have invaded islands of all sizes within the archipelago (Fig. 2), with black rats establishing populations on some of the smallest islands (0.04 ha.). In contrast, fish, amphibians, and reptiles are only found on islands greater than 15,000 ha. For all islands where the status of alien vertebrates is confirmed, the number of species tends to increase on islands with an area greater than 1000 ha (Fig. 3a). However, when islands inhabited by humans are removed, there is little relationship between island size and the number of alien vertebrates (Fig. 3b).

The first vertebrates introduced to the Galápagos (Snodgrass & Heller, 1899; Hunter, 1906; Patton *et al.*, 1975; Hoeck, 1984), alien mammals, remain the most numerous (Fig. 4). New introductions of mammals have continued from before 1800 though today, but three periods predominate. During the early 1830s, the first human settlement in the Galápagos on Floreana was being established and in this period six species of alien mammal were introduced (Hoeck, 1984). Alien mammals again increased markedly in the 1930s with three introductions (Slevin, 1931; Conway & Conway, 1947) then in the 1960s with another three species (Kastdalen, 1982). Alien birds were first recorded in the late 1800s (Wolf, 1879; in Baur, 1891), with chickens reported from Floreana, but domestic fowl most likely arrived with the first human inhabitants. The rate of intentional introduction of mammals has declined in the last 50 years, but bird and reptile introductions are on the rise (Fig. 4). Introductions are also increasing of small, cryptic species that easily hitchhike on cargo, such as frogs.

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 & 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 & Courtenay Jr., 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 & Mayden, 2004). Tilapia were eradicated from Laguna Junco in 2007 using rotenone (Leo Nico U. S. Geological Survey, personal communication).

Pacific fat sleeper (*Dormitator latifrons*) – This fish was first reported from the Galápagos in 1992 (Massay & 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 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 GNP opened a channel from the lagoon to the sea to increase the salinity in the lagoon (see Tree frog 3 below; Alex Hearn, personal communication CDRS).

Amphibians

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

Tree frog 1 (*Eleutherodactylus unistrigatus*) – Reported from Isabela (CDRS internal records).

Tree frog 2 (*Hyla* sp.) – Reported from San Cristóbal in 1990 (CDRS internal records).

Tree frog 3 (*Scinax quinquefasciata*) – This frog is thought to have arrived during the 1997-1998 El Niño, and has since been in Puerto Ayora and Puerto Villamil. It has established breeding populations in the lagoons to the west of Villamil. The frog is a predator of invertebrates and there is concern the frogs will impact the native species in the lagoons. Spraying a caffeine solution on the frogs has been used as a control method and in 2005 the GNP created a channel from the sea into the lagoon to increasing the salinity of the lagoon (Alex Hearn, personal communication CDRS).

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 GNP (Jiménez-Uzcátegui *et al.*, 2007).

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 2 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, 1983b; 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, 1983b; Olmedo & Cayot, 1994). However, it has spread into the highlands and is now found in the community of El Progresso, the surrounding farmland, and national park in higher numbers (Hoogmoed, 1989; Olmedo & 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 (Olmedo & Cayot, 1994; Wright, 1983b; Hoogmoed, 1989). 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, 1983a; Altamirano, 2002), probably arriving via shipping from Guayaquil (Hoogmoed, 1989). It has since spread to Villamil and Puerto Baquerizo Moreno (Olmedo & 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. galapagoensis* were studied and it appears the mourning gecko is not affecting the native species (Altamirano, 2002).

San Cristóbal leaf-toed gecko (*Phyllodactylus leei*) – This species is endemic to San Cristóbal, but was found in Villamil (Wood, 1939). There have been no further reports of this species on Isabela, or elsewhere outside its natural range (Olmedo & Cayot, 1994). This species is not included in trend analyses.

Peter's leaf-toed gecko (*P. reissi*) – Found only in Puerto Ayora, this species was first recorded in 1975 (Olmedo & Cayot, 1994; Hoogmoed, 1989). 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 & Cayot, 1994; Altamirano, 2002). Despite its range expansion, *P.*

reissi appears to be dependent on urban habitat, having not 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 & Cayot, 1994). In urban habitats, *P. reissi* does displace the native gecko, *P. galapagoensis*, though the mechanism is unclear (Altamirano, 2002).

<u>Leaf-toed gecko</u> (*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 & 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 lists 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 & 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 A or trend analyses.

<u>Five-lined skink</u> (*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).

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 & 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.

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).

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 & Conway, 1947). After 4 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 & 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).

<u>Domestic turkey</u> (*Meleagris gallopavo*) – A male and female turkey were introduced to Santiago in 1937 (Conway & Conway, 1947). After 4 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 from farms on Isabela, San Cristóbal and Santa Cruz (Jiménez-Uzcátegui *et al.*, 2007). No wild populations are known.

<u>Cattle egret</u> (*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 & de Vries, 1993). However, they have recently been categorized as aliens by the GNP & CDRS, because their colonization was likely facilitated by the alteration of the habitat from introduced alien grazers (Telfair, 1994; Weber, 1972). Cattle egrets have been sighted on most islands (Appendix B; 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 (RBP, personal observation). In Portugal, pastureland within 5 km of nesting sites was critical to breeding success of cattle egrets (Farinha & Leitao, 1996). Cattle egrets are not documented to have large scale impacts on native wildlife in the Galápagos, but the potential exists. Introduced populations of cattle egrets often comprise the dominant species of waterbird in nesting colonies (Bryan *et al.*, 2003; Dugger *et al.*, 2005) and in Australia a colony of about 50 pairs grew to about 3,500 in 3 years (McKilligan, 1997). In general, cattle egrets have a catholic diet, which includes terrestrial and marine invertebrates, fish, reptiles and rodents (Gassett *et al.*, 2000; Siegfried, 1971) and in Hawaii they prey on chicks of native waterbirds, such as black-necked stilts (*Himanotpus mexicanus*; Stone & 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.

<u>Rock pigeon</u> (*Columba livia*) – Four rock pigeons were brought to Floreana Island 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 (Appendix B). 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 GNP and locals (Phillips *et al.*, 2003). By the early 2000s, feral rock pigeons comprised the majority of the population in the three principal towns and lofts had become established in the highlands of San Cristóbal and Santa Cruz. In Puerto Ayora, rock pigeons were nesting on cliffs on the town and national park border, while in Puerto Baquerizo Moreno, they were nesting in abandoned buildings. Locals in the Galápagos valued rock pigeons for several reasons, including feeding and watching, but they also prized them as food items, believing them to benefit health and mental well-being (RBP, personal observation). Though no impacts to the native fauna from rock pigeons have been documented, rock pigeons likely transmitted *Trichomonas gallinae* to the endemic Galápagos dove. Transmission of additional and more virulent diseases posed a serious threat to avifauna of Galápagos (Phillips *et al.*, 2003). The GNP 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).

<u>Red-masked parakeet</u> (*Aratinga erythrogenys*) – In April 1996, locals reported two to three feral parrots 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).

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 & 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 & de Vries, 1993), but following their arrival are now widely distributed on islands in the archipelago (Appendix B). 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 & Bensted-Smith, 2000). 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). Concomitantly, an increase in ani numbers was observed on Santa Cruz and Alcedo Volcano, Isabela. 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 remove anis from Fernandina and Genovesa Islands 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

Monkey – Three individuals of an unidentified species of monkey (Appendix C) were reported from Floreana in the 1930s (Duffy, 1981). They all died of unspecified causes.

Cotton-top tamarin (*Saguinus oedipus*) – In 2006, a pet monkey was discovered on a private boat at San Cristóbal.

Feral cat (*Felis catus*) – Cats invaded all inhabited islands and at one time established domestic and feral populations (Appendix C). 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). And on Venecia, 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), which at 2620 ha is the fourth largest island worldwide from which cats have been eradicated (Nogales *et al.*, 2004). 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.

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 & 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.

Feral dog (*Canis lupus familiaris*) – Domestic dogs are found in urban and rural areas on all the inhabited islands, including Baltra (Appendix C). 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 & 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 Fe 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, have 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 is now 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 & Johnson, 1985). Donkeys also impact tortoises and land iguanas by trampling their nests (Fowler de Neira & 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 & Mauchamp, 1995). Sporadic control of donkeys on Santiago and Alcedo Volcano has been conducted for decades (Carrion *et al.*, 2007)(Carrion et al. 2007). In 2004 and 2005, respectively, donkeys were eradicated in conjunction with eradication campaigns on goats and pigs (see below; Carrion *et al.*, 2007). On the remaining islands where donkeys are present, occasional hunting by locals and culling by GNP occurs.

Feral horse (*E. caballus*) – Horses are found on all inhabited islands, except Baltra (Appendix C; Hoeck, 1984). Feral populations have established only on the volcano, Sierra Negra, Isabela. Locals capture juveniles occasionally for domestication, which may limit population size.

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*) tortoises (Green, 1979; in Coblentz & Baber, 1987; MacFarland *et al.*, 1974). On Santiago, pigs were a probable factor in the extinction of land iguanas (Coblentz & 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 aid spread invasive plants by consuming and dispersing their seeds (e.g. guava; Coblentz & 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 & 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.

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

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 to 30,000 on southern Isabela's Volcan Cerro Azul. On Sierra Negra, self-sustaining herds of domestic and semi-feral 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, diminished stream-flow from a crater lake. 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 & Black, 1983; Schultz, 2003). During the 1970s and 80s, hunting by locals and culling by GNP eliminated feral populations on all islands but Isabela. The GNP has encouraged ranchers to maintain fences on Floreana, San Cristóbal, and Santa Cruz, which has reduced the problem of feral cattle reestablishing in the park areas (Schofield, 1989).

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). Goats were also briefly introduced to Plaza Sur, in the 1960s but were eradicated within one to two months (Craig MacFarland 1977, Colorado State University, personal communication). In 1990, they were discovered on tiny (1.3 ha) Marielas Sur (Campbell & Donlan, 2005). The impact of goats on Galápagos' biota is well documented (Hamann, 1984; Schofield, 1989). High population densities and heavy 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. Fortunately, the GNP has been successful in eradicating goats from many islands (Appendix C; Campbell & Donlan, 2005).

<u>Domestic sheep</u> (*Ovis aries*) – Feral sheep do not occur in the Galápagos, but sheep are found on farms on Santa Cruz, and possibly San Cristóbal and Isabela. 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 on Socorro Island, Revillagigedos (18°N; Walter & Levin, 2008) and at one time were found on several of the Channel Islands, California, USA (33° N; Klinger *et al.*, 2002; Jorgensen & Ferguson, 1984). In these archipelagos, feral sheep grazing severely degraded the habitat.

House mouse (*Mus musculus*) – House mice were first recorded on San Cristóbal in 1899 (Snodgrass & Heller, 1899) and Floreana and Santiago Islands 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 island 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 1982-83, 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 & 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 & Muñoz Heredia, 1994). Currently, we document mice present on eight islands (Appendix C). 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).

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 4 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 & 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 Garraptero (this study). 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).

<u>Black rat</u> (*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 WWII. 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 (1994) reported black rat as present on 10 islands total. Our work reveals black rats have invaded at least 37 islands, although some populations have been eradicated (Appendix C). This includes three of the five islands in the brackish lake on Isabela.

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 & Cruz, 1987). Circumstantial evidence suggests black rats were a factor in the extinction of several species of native Galápagos rodents (reviewed inClark, 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 C). However, Hoeck's prediction is fortunately proving not to be accurate. 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 4.6 ha. (Appendix C), with one failed attempt on Bainbridge 1 (1.4 ha). Currently, an eradication campaign is underway on Seymour Norte (183.9 ha; Javier Zabala, CDRS, personal communication).

<u>Guinea pig</u> (*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 & Conway, 1947). In 1965, CDRS records report of 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 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.

<u>European rabbit</u> (*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. Fortunately, rabbits have not established feral populations. Introductions of rabbits frequently succeed

(Flux & 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

In 1984, 13 species of alien vertebrate were reported in the Galápagos (Hoeck, 1984). Twenty five years later, 42 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, 1983b; Wright, 1983a). However, the increase in alien vertebrates from 1984 to 2008 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 more than three to one. And two new categories of vertebrates, amphibians and freshwater fishes, have invaded. Surprisingly, the most diverse native vertebrates, reptiles and birds, are the least impacted. 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 GNP has demonstrated its ability to eradicate these animals on a very large scale and the risk of reinvasion is low (Campbell *et al.*, 2004; Cruz *et al.*, 2005; Carrion *et al.*, 2007). In contrast, alien rats, also highly damaging, are more difficult to eradicate and pose a greater risk of reinvasion (Howald *et al.*, 2007). Interestingly, house mice appear poor invaders in the Galápagos, either by hitchhiking or natural colonization. Since their introduction to the archipelago more than 100 years ago, mice have invaded less than 10% of the islands. Compare this to black rats, which have invaded 30% of the islands. Alien geckos also appear to be poorly adapted to invading new islands within the Galápagos. Despite arriving 100 or more years ago, the shieldhead gecko has failed to colonize any islands other than San Cristóbal and Peter's leaf-toed gecko remains restricted to Santa Cruz. This is not surprising given the Galápagos are the only island group these two species have invaded (Lever, 2003). The mourning gecko, a cosmopolitan invader of islands, is still restricted to 3 islands after 40 years. However, because it is parthenogenetic and adapted to live in mangroves, it has a greater potential to invade other islands (Altamirano, 2002).

The future of new vertebrate invasions to the Galápagos is likely to continue shifting away from the intentional introduction of large species (e.g. goats and chickens) and toward hitchhiking cryptic species (e.g. frogs); however, the introduction of pets and novelty species (e.g. monkeys and iguanas) will remain a problem. 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 & Savidge, 2007).

Conclusions and recommendations

We have shown that new alien species continue to invade the Galápagos. In fact, the rate of arrival is increasing (Fig. 4). In 2006 alone, two turtle species, a green iguana, and monkey were reported. This is occurring despite the establishment of a quarantine system within the Galápagos. Obviously, more work needs to be done to improve inspection and enforcement protocols. Equally urgent is the need to manage the risk of inter-island invasion by currently established alien vertebrate species. Of particular concern are alien rodents, which have invaded many islands within the archipelago, but most remain alien rodent free. These latter islands are critical to the survival of many vulnerable endemic species, none more so than Fernandina and Santa Fé, which harbor three of the four extant species of native rice rat (Dowler *et al.*, 2000). The GNP has taken great strides in the eradication of alien vertebrates and continues to do so, but some caution in proceeding too quickly is warranted. Black rats appear able to invade islands separated by hundreds of meters without the aid of human transport (R. B. Phillips, in prep.). The risk of reinvasion should be evaluated before committing resources to large-scale rodent eradications (Abdelkrim *et al.*, 2005). Finally, it is necessary to consider how factors, such as global climate change will affect the dynamics of alien vertebrate invasions in the Galápagos. We have seen that El Niño events can improve environmental conditions for some species allowing them to establish on new islands and in new areas. If the Galápagos environment becomes less arid we can expect to see an increase in the number of invasions of frog species, as well as a range expansion of those species within the archipelago. Managing the threat posed by alien vertebrates to the Galápagos requires combining effective eradication and quarantine programs, but to stem the tide of alien invasions it is critical to understand the changing nature of introductions in the face of a rapidly growing human population.

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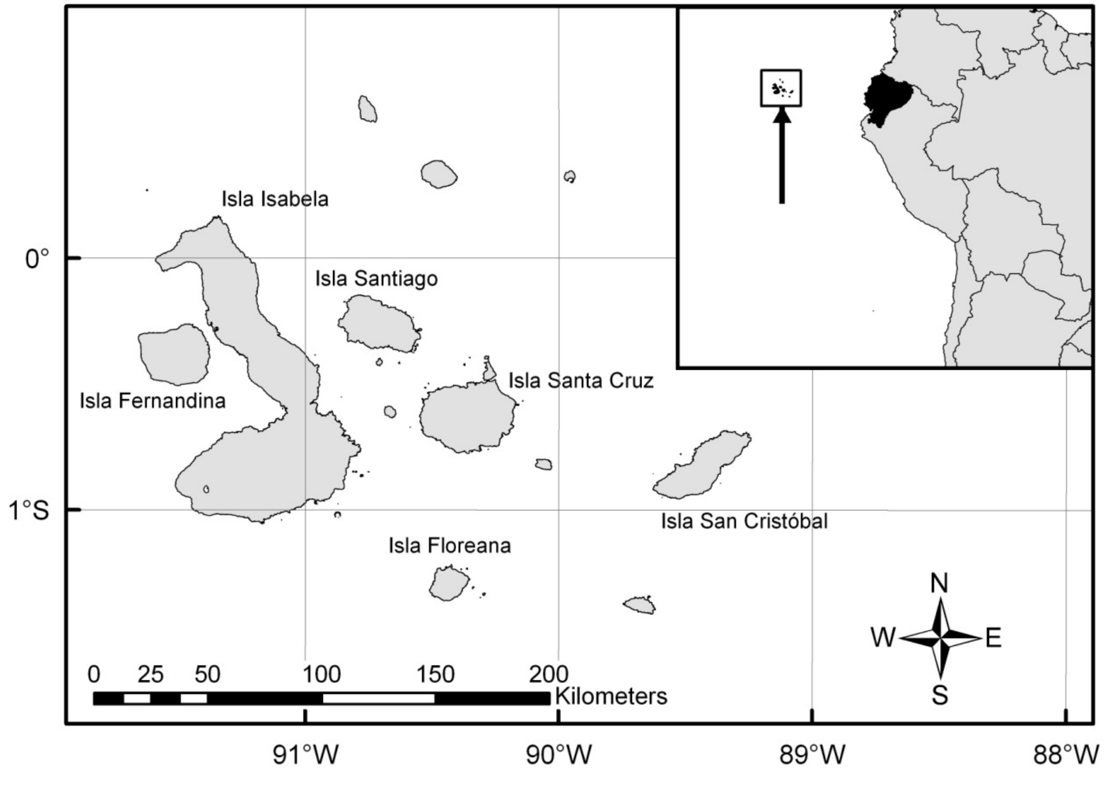


Figure 1 The Galápagos archipelago of Ecuador and its location relative to South America.

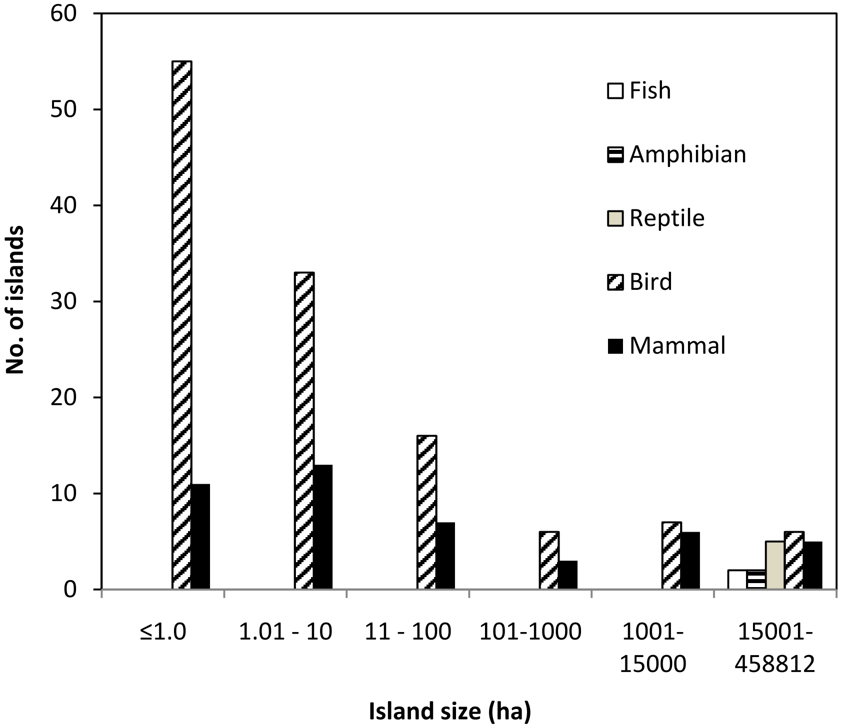
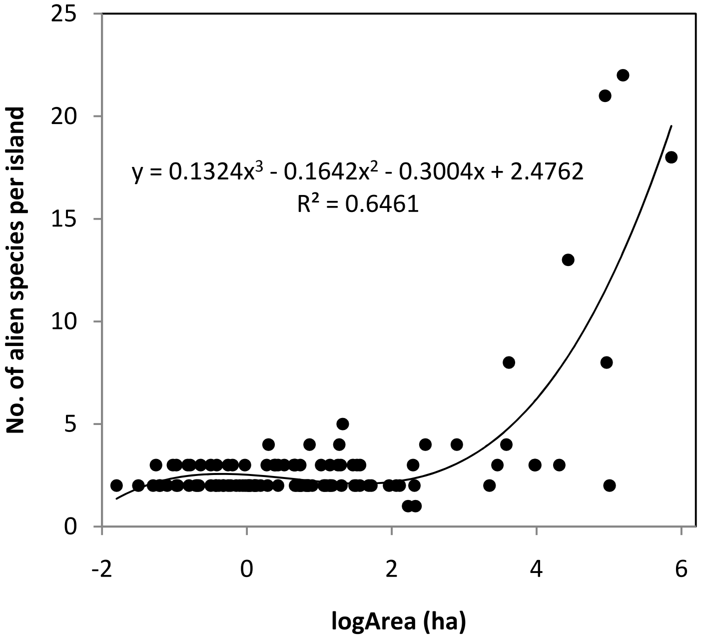


Figure 2 Number of islands within various size ranges on which alien vertebrates have invaded and established. Analysis includes islands where populations of alien species currently occur and islands where populations have been eradicated or gone extinct.

a) All islands



b) Uninhabited islands

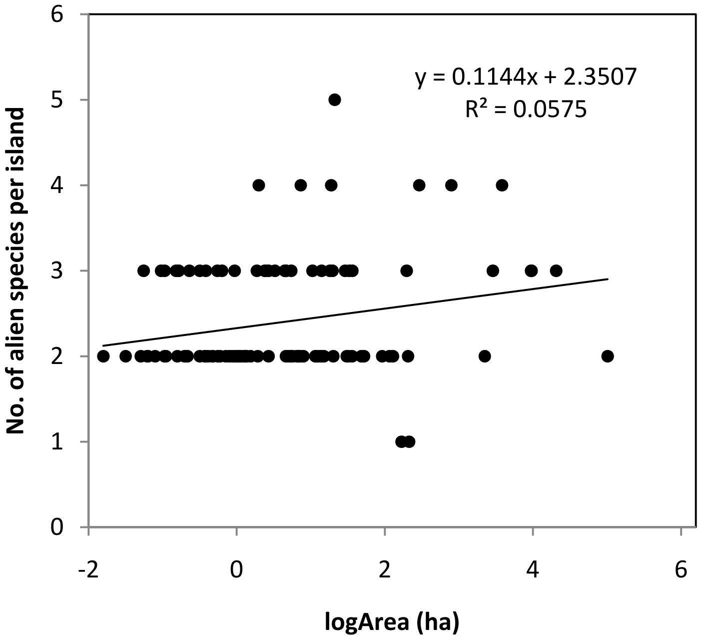


Figure 3 Distribution of the number of species of alien vertebrates on all islands (a) and uninhabited islands (b) in the archipelago. Island size is on a $\log_{10}$ scale and the regression line is a third-order polynomial. Analysis includes currently occurring, extinct, and eradicated species.

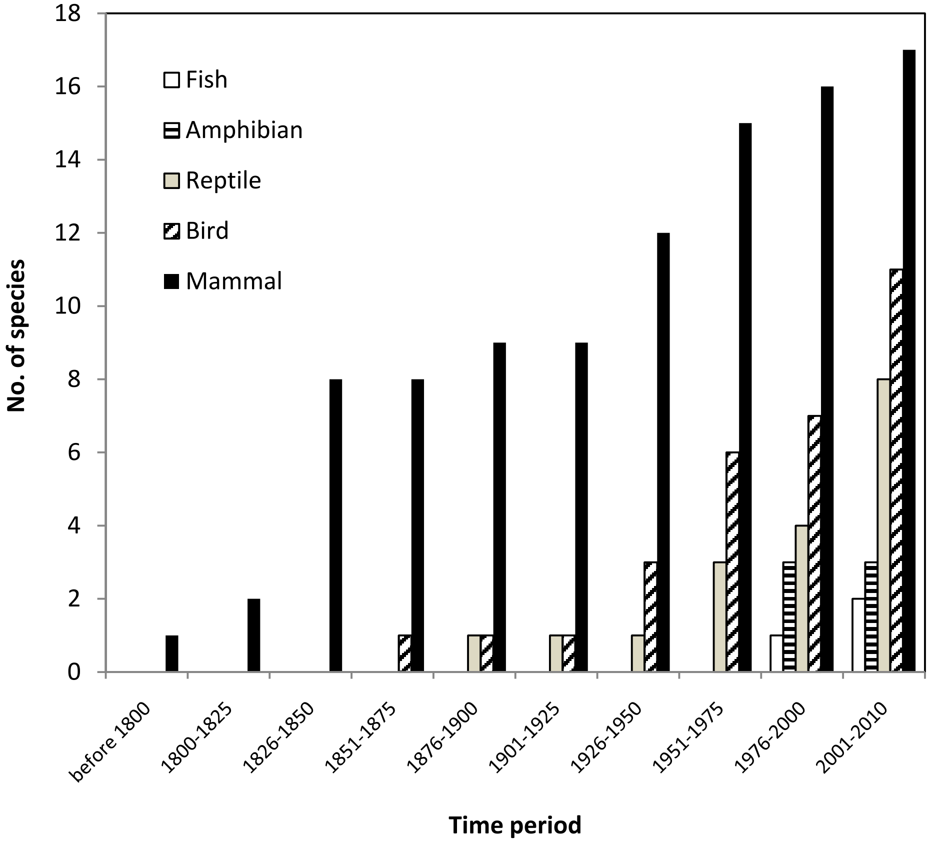


Figure 4 Cumulative number of alien species within each vertebrate Class introduced to the archipelago during a distinct period from before 1800 to present. Analysis includes confirmed and reported arrivals. One reptile and one amphibian species lack dates of arrival and are omitted. One reptile is an intra-archipelago movement and also omitted.

Appendix A List of alien fish, amphibian, and reptile species and their status on islands in the Galápagos archipelago.

Island		Fish		Amphibian				Reptile								
Name	Size (ha)	ORNI	DOLA	CHMA	ELUN	HY sp.	SCQU	GEDE	TRSC	POUN	IGIG	GOCA	LELU	PHLE	PHRE	EUIN
Isabela	458812		P		R		P						P	E		
Santa Cruz	98555						P	R	I		R		P		P	
Fernandina	64248															
Santiago	58465															
San Cristóbal	55809	X		R		R	R			I	I	P	P			I
Floreana	17253															
Marchena	12996															
Española	6048.0															
Pinta	5940.0															
Baltra	2619.6											R				
Santa Fé	2413.0															
Pinzón	1815.0															
Genovesa	1410.8															
Rábida	499.31															
Seymour Norte	183.89															
Wolf	134.40															
Tortuga	129.90															
Bartolomé	124.48															
Darwin	106.30															
Gardner por Floreana	81.17															
Cuatro Hermanos Sur	72.93															
Gardner por Española	58.04															
Daphne Major	33.02															
Cuatro Hermanos #2	30.41															
Eden	23.02															
Caldwell	22.84															
Sombrero Chino	20.88															
Cuatro Hermanos O.	20.42															
Enderby	19.30															
Bainbridge #3	18.34															
Venecia	13.28															
Albany	12.73															
Tintorera (I)	12.43															
Plaza Sur	11.90															
Bainbridge #1	11.42															
Campéon	9.51															
Norte de Wolf	9.00															
Plaza Norte	8.84															
Beagle Sur	8.73															
Daphne Chica	7.96															
Sin Nombre	7.53															
Cuatro Hermanos E.	7.26															
Lobos	6.67															
Leon Dormido	5.02															
Mosquera	4.63															
Caamaño	4.50															
Bainbridge #6	4.48															
Redonda	4.31															
Beagle Oeste	4.26															
Bainbridge #5	4.07															

Island		Fish		Amphibian				Reptile								
Name	Size (ha)	ORNI	DOLA	CHMA	ELUN	HY sp.	SCQU	GEDE	TRSC	POUN	IGIG	GOCA	LELU	PHLE	PHRE	EUIN
Tortuga Oeste	3.57															
Cowley	3.50															
Bainbridge #4	3.44															
Guy Fawkes Oeste	3.40															
Guy Fawkes Sur	3.29															
Watson	3.05															
Punta Bowditch Norte	2.92															
Gordon Este	2.91															
Bainbridge #2	2.90															
Villamil Sureste (J)	2.81															
La Loberia	2.37															
Las Bayas Grande	2.07															
Osborn	1.70															
Cráter Beagle #2	1.70															
Cráter Beagle #1	1.56															
Punta Bowditch Sur	1.51															
Marielas Sur	1.25															
Guy Fawkes Este	1.22															
Fondiadero (H)	1.18															
Leon Dormido P.	0.98															
Cousins	0.86															
Gordon Oeste	0.83															
Dalrymple	0.80															
Bainbridge #7	0.80															
Este	0.74															
Beagle Norte	0.71															
Viuda	0.68															
Santa Fé	0.67															
Bainbridge #8	0.65															
Cráter Cerro Azul	0.60															
Muelle (K)	0.59															
Xarifa	0.55															
Pitt (nearshore)	0.50															
Ayora	0.50															
Corona del Diablo G.	0.45															
Pitt (offshore)	0.40															
Oeste	0.38															
Espejo	0.36															
de Canal Sur	0.35															
Punta Bowditch Este	0.35															
Blanca	0.30															
Devine	0.30															
Faro (G)	0.30															
La Botella	0.27															
Gordon Central	0.26															
Marielas Norte	0.24															
Guy Fawkes Norte	0.24															
El Arco	0.20															
Logie	0.20															
Las Bayas Pequeña	0.15															
Caleta Tiburon Norte	0.14															
Las Cuevas Este	0.13															
Mao	0.13															

Island		Fish		Amphibian				Reptile								
Name	Size (ha)	ORNI	DOLA	CHMA	ELUN	HY sp.	SCQU	GEDE	TRSC	POUN	IGIG	GOCA	LELU	PHLE	PHRE	EUIN
Caleta Tiburón Sur	0.10															
El Torre	0.10															
La Ventana	0.10															
Dumb	0.10															
Las Cuevas Oeste	0.10															
Cráter Beagle #5	0.10															
Noroeste de Santa Fe	0.07															
Corona del Diablo O.	0.07															
Marielas Este	0.07															
Cráter Beagle #3	0.07															
Onan	0.06															
Union	0.05															
El Trompo	0.04															
Corona del Diablo E.	0.04															
Gran Felipe	0.04															
Rata	0.04															
Cráter Beagle #4	0.03															
Caleta Bucanero	0.02															
Corona del Diablo C.	0.02															
Ballena	0.01															

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*).

Presence Codes - E = extinct; I = intercepted; P = present; R = reported, X = eradicated; blanks indicate absence of a species.

Appendix B List of alien bird species and their status on islands in the Galápagos archipelago.

Island		Bird										
Name	Size (ha)	ANAN	DUCK	NUME	CO sp.	PAMU	GAGA	MEGA	BUIB	COLI	ARER	CRAN
Isabela	458812		P	R	R		P	P	P	X		P
Santa Cruz	98555		P	P	R		P	P	P	X		P
Fernandina	64248								P			E
Santiago	58465		X				X	E	P			P
San Cristóbal	55809	R	P	R	R	R	P	P	P	X	E	P
Floreana	17253		X	R	R		P	E	P	E		P
Marchena	12996								P			P
Española	6048.0								P			P
Pinta	5940.0								P			P
Baltra	2619.6						P		P			P
Santa Fé	2413.0								P			P
Pinzón	1815.0								P			P
Genovesa	1410.8								P			E
Rábida	499.31								P			P
Seymour Norte	183.89								P			P
Wolf	134.40								P			
Tortuga	129.90								P			P
Bartolomé	124.48								P			P
Darwin	106.30								P			
Gardner por Floreana	81.17								P			E
Cuatro Hermanos Sur	72.93								P			P
Gardner por Española	58.04								P			P
Daphne Major	33.02								P			P
Cuatro Hermanos #2	30.41								P			P
Eden	23.02								P			P
Caldwell	22.84								P			P
Sombrero Chino	20.88								P			P
Cuatro Hermanos O.	20.42								P			P
Enderby	19.30								P			P
Bainbridge #3	18.34								P			P
Venecia	13.28								P			P
Albany	12.73								P			P
Tintorera (I)	12.43								P			P
Plaza Sur	11.90								P			P
Bainbridge #1	11.42								P			P
Campéon	9.51								P			E
Norte de Wolf	9.00								P			
Plaza Norte	8.84								P			P
Beagle Sur	8.73								P			P
Daphne Chica	7.96								P			P
Sin Nombre	7.53								P			P
Cuatro Hermanos E.	7.26								P			P
Lobos	6.67								P			P
Leon Dormido	5.02								P			P

Island		Bird										
Name	Size (ha)	ANAN	DUCK	NUME	CO sp.	PAMU	GAGA	MEGA	BUIB	COLI	ARER	CRAN
Mosquera	4.63								P			P
Caamaño	4.50								P			P
Bainbridge #6	4.48								P			P
Redonda	4.31								P			P
Beagle Oeste	4.26								P			P
Bainbridge #5	4.07								P			P
Tortuga Oeste	3.57								P			P
Cowley	3.50								P			P
Bainbridge #4	3.44								P			P
Guy Fawkes Oeste	3.40								P			P
Guy Fawkes Sur	3.29								P			P
Watson	3.05								P			P
Punta Bowditch Norte	2.92								P			P
Gordon Este	2.91								P			P
Bainbridge #2	2.90								P			P
Villamil Sureste (J)	2.81								P			P
La Loberia	2.37								P			P
Las Bayas Grande	2.07								P			P
Osborn	1.70								P			P
Cráter Beagle #2	1.70								P			P
Cráter Beagle #1	1.56								P			P
Punta Bowditch Sur	1.51								P			P
Marielas Sur	1.25								P			P
Guy Fawkes Este	1.22								P			P
Fondiadero (H)	1.18								P			P
Leon Dormido P.	0.98								P			P
Cousins	0.86								P			P
Gordon Oeste	0.83								P			P
Dalrymple	0.80								P			P
Bainbridge #7	0.80								P			P
Este	0.74								P			P
Beagle Norte	0.71								P			P
Viuda	0.68								P			P
Santa Fé	0.67								P			P
Bainbridge #8	0.65								P			P
Cráter Cerro Azul	0.60								P			P
Muelle (K)	0.59								P			P
Xarifa	0.55								P			P
Pitt (nearshore)	0.50								P			P
Ayora	0.50								P			P
Corona del Diablo G.	0.45								P			P
Pitt (offshore)	0.40								P			P
Oeste	0.38								P			P
Espejo	0.36								P			P
de Canal Sur	0.35								P			P
Punta Bowditch Este	0.35								P			P
Blanca	0.30								P			P

Island		Bird										
Name	Size (ha)	ANAN	DUCK	NUME	CO sp.	PAMU	GAGA	MEGA	BUIB	COLI	ARER	CRAN
Devine	0.30								P			P
Faro (G)	0.30								P			P
La Botella	0.27								P			P
Gordon Central	0.26								P			P
Marielas Norte	0.24								P			P
Guy Fawkes Norte	0.24								P			P
El Arco	0.20								P			
Logie	0.20								P			P
Las Bayas Pequeña	0.15								P			P
Caleta Tiburon Norte	0.14								P			P
Las Cuevas Este	0.13								P			P
Mao	0.13								P			P
Caleta Tiburón Sur	0.10								P			P
El Torre	0.10								P			
La Ventana	0.10								P			
Dumb	0.10								P			P
Las Cuevas Oeste	0.10								P			P
Cráter Beagle #5	0.10								P			P
Noroeste de Santa Fe	0.07								P			P
Corona del Diablo O.	0.07								P			P
Marielas Este	0.07								P			P
Cráter Beagle #3	0.07								P			P
Onan	0.06								P			P
Union	0.05								P			P
El Trompo	0.04								P			P
Corona del Diablo E.	0.04								P			P
Gran Felipe	0.04								P			P
Rata	0.04								P			P
Cráter Beagle #4	0.03								P			P
Caleta Bucanero	0.02								P			P
Corona del Diablo C.	0.02								P			P
Ballena	0.01								P			P

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*).

Presence Codes - E = extinct; P = present; R = reported, X = eradicated; blanks indicate absence of a species.

Appendix C List of alien mammal species and their status on islands in the Galápagos archipelago.

Island		Mammal																
Name	Size (ha)	MONK	SAOE	FECA	LEPA	CALU	EQAS	EQCA	SUSC	DEER	BOTA	CAHI	OVAR	MUMU	RANO	RARA	CAPO	ORCU
Isabela	458812			P		P	P	P	P		P	P	R	P		P	R	
Santa Cruz	98555			P		P	P	P	P		P	P	P	P	P	P	P	R
Fernandina	64248																	
Santiago	58465			R	X	X	X		X			X		P		P	E	
San Cristóbal	55809		I	P		P	P	P	P	E	P	P	R	P	P	P	R	P
Floreana	17253	E		P		P	P	P	P		P	P		P		P	R	
Marchena	12996											X						
Española	6048.0											X						
Pinta	5940.0											X						
Baltra	2619.6			X		P						P		P		P		
Santa Fé	2413.0					X						X						
Pinzón	1815.0															P		
Genovesa	1410.8																	
Rábida	499.31											X			P			
Seymour Norte	183.89													E		P		
Wolf	134.40																	
Tortuga	129.90																	
Bartolomé	124.48															P		
Darwin	106.30																	
Gardner por Floreana	81.17																	
Cuatro Hermanos Sur	72.93																	
Gardner por Española	58.04																	
Daphne Major	33.02																	
Cuatro Hermanos #2	30.41													U	U	U		
Eden	23.02															P		
Caldwell	22.84																	
Sombrero Chino	20.88															P		
Cuatro Hermanos O.	20.42													U	U	U		
Enderby	19.30																	
Bainbridge #3	18.34															P		
Venecia	13.28			X		E										P		
Albany	12.73																	
Tintorera (I)	12.43															P		
Plaza Sur	11.90											X		P				
Bainbridge #1	11.42															P		
Campéon	9.51																	
Norte de Wolf	9.00																	
Plaza Norte	8.84													P				
Beagle Sur	8.73																	
Daphne Chica	7.96																	
Sin Nombre	7.53																	
Cuatro Hermanos E.	7.26													U	U	U		
Lobos	6.67															P		
Leon Dormido	5.02													U	U	U		

Island		Mammal																
Name	Size (ha)	MONK	SAOE	FECA	LEPA	CALU	EQAS	EQCA	SUSC	DEER	BOTA	CAHI	OVAR	MUMU	RANO	RARA	CAPO	ORCU
Mosquera	4.63													E		X		
Caamaño	4.50																	
Bainbridge #6	4.48																	
Redonda	4.31													U	U	U		
Beagle Oeste	4.26																	
Bainbridge #5	4.07																	
Tortuga Oeste	3.57																	
Cowley	3.50													U	U	U		
Bainbridge #4	3.44															X		
Guy Fawkes Oeste	3.40																	
Guy Fawkes Sur	3.29																	
Watson	3.05													U	U	U		
Punta Bowditch Norte	2.92															P		
Gordon Este	2.91													U	U	U		
Bainbridge #2	2.90															P		
Villamil Sureste (J)	2.81															P		
La Loberia	2.37													U	U	U		
Las Bayas Grande	2.07			X														
Osborn	1.70																	
Cráter Beagle #2	1.70															P		
Cráter Beagle #1	1.56															P		
Punta Bowditch Sur	1.51															P		
Marielas Sur	1.25											X				X		
Guy Fawkes Este	1.22																	
Fondiadero (H)	1.18															P		
Leon Dormido P.	0.98													U	U	U		
Cousins	0.86																	
Gordon Oeste	0.83													U	U	U		
Dalrymple	0.80													U	U	U		
Bainbridge #7	0.80																	
Este	0.74													U	U	U		
Beagle Norte	0.71																	
Viuda	0.68													U	U	U		
Santa Fé	0.67																	
Bainbridge #8	0.65																	
Cráter Cerro Azul	0.60													U		U		
Muelle (K)	0.59															P		
Xarifa	0.55																	
Pitt (nearshore)	0.50													U	U	U		
Ayora	0.50																	
Corona del Diablo G.	0.45																	
Pitt (offshore)	0.40															P		
Oeste	0.38																	
Espejo	0.36													U	U	U		
de Canal Sur	0.35													U	U	U		
Punta Bowditch Este	0.35															P		

Island		Mammal																
Name	Size (ha)	MONK	SAOE	FECA	LEPA	CALU	EQAS	EQCA	SUSC	DEER	BOTA	CAHI	OVAR	MUMU	RANO	RARA	CAPO	ORCU
Blanca	0.30													U	U	U		
Devine	0.30																	
Faro (G)	0.30													U	U	U		
La Botella	0.27													U	U	U		
Gordon Central	0.26													U	U	U		
Marielas Norte	0.24															P		
Guy Fawkes Norte	0.24																	
El Arco	0.20													U	U	U		
Logie	0.20															X		
Las Bayas Pequeña	0.15			X														
Caleta Tiburon Norte	0.14													U	U	U		
Las Cuevas Este	0.13																	
Mao	0.13																	
Caleta Tiburón Sur	0.10															P		
El Torre	0.10													U	U	U		
La Ventana	0.10													U	U	U		
Dumb	0.10																	
Las Cuevas Oeste	0.10																	
Cráter Beagle #5	0.10															P		
Noroeste de Santa Fe	0.07													U	U	U		
Corona del Diablo O.	0.07																	
Marielas Este	0.07															X		
Cráter Beagle #3	0.07																	
Onan	0.06															P		
Union	0.05													U	U	U		
El Trompo	0.04															U		
Corona del Diablo E.	0.04																	
Gran Felipe	0.04																	
Rata	0.04															P		
Cráter Beagle #4	0.03																	
Caleta Bucanero	0.02																	
Corona del Diablo C.	0.02																	
Ballena	0.01													U	U	U		

Species Code - MONK (Monkey sp.), SAOE (*Saguinus oedipus*), FECA (*Felis catus*), LEPA (*Leopardus pardalis*), CALU (*Canis lupus familiaris*), EQAS (*Equus asinus*), EQCA (*E. caballus*), SUSC (*Sus scrofa*), DEER (Deer sp.), BOTA (*Bos taurus*), CAHI (*Capra hircus*), OVAR (*Ovis aries*), MUMU (*Mus musculus*), RANO (*Rattus norvegicus*), RARA (*R. rattus*), CAPO (*Cavia porcellus*), ORCU (*Oryctolagus cuniculus*).

Presence Codes - E = extinct; I = intercepted; P = present; R = reported, U = unknown; X = eradicated; blanks indicate absence of a species.

CHAPTER 2

EFFECT OF AREA AND ISOLATION ON INCIDENCE OF ALIEN RODENTS IN THE GALÁPAGOS ISLANDS

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ABSTRACT

The role of landscape features in structuring insular communities of animals has been a focus of biogeographic investigations for decades, however the relative importance of key factors remain unclear. In this study we used a species-based model to examine the influence of island area and isolation on the distribution patterns of three species of alien rodents. We determined the probability of a rodent occurring on an island and the importance of immigration and persistence in their incidence on an island. We predicted that isolation will have a reduced effect on the distribution of alien species because of their commensal habits. We obtained presence/absence data for 81 islands in the Galápagos archipelago. Using logistic regression and Akaike's Information Criterion (AIC), we compared five a priori models (random, minimum area, maximum isolation, block, or compensatory) to identify the which pattern best described a rodent species distribution. We conducted analyses at two scales: archipelago-wide and individual source/satellite islands. We analyzed the distributions for two rodent species, black rats (*Rattus rattus*) and house mice (*Mus musculus*). At the archipelago-wide scale, black rats exhibited a compensatory distribution, with area and isolation having equal influence on their occurrence on an island. Results for house mice were mixed, but area and isolation both affect their occurrence on an island. At the smaller scale the influence of area on the distribution of black rats was reduced, with distance from source island the predominant factor affecting occurrence on an island. We refuted our hypothesis that isolation would have reduced influence on alien rodent incidence on an island. At a large scale, the occurrence of both black rats and house mice appears to be driven equally by the ability to immigrate an island and to persist upon reaching the island. Examined at a smaller scale, isolation appears to be the key factor determining the incidence of black rats on an island, suggesting they can persist on some of the smallest islands (0.04 ha) in the archipelago.

INTRODUCTION

At its most fundamental level, biogeography is the study of patterns of species distributions across landscape gradients (Brown & Lomolino, 1998). A prominent pattern in island biogeography, and the foundation of the equilibrium theory of island biogeography (ETIB), is the tendency for larger and less isolated islands to have greater species richness (MacArthur & Wilson, 1963; MacArthur & Wilson, 1967; also see Triantis *et al.*, 2008). A corollary of the ETIB is the probability that a particular species occurs on an island is a function of island area and isolation, or their interaction (Schoener & Schoener, 1983; Diamond, 1975). Lomolino (1986; 2000) proposed a theory of insular species composition and developed a model to examine the relative influence of area and isolation on the insular distribution of species. Use of this species-based model may provide insight into the immigration and persistence abilities of species and the dynamics of colonization and extinction, respectively (Gilpin & Diamond, 1981; Adler & Wilson, 1985; Peltonen & Hanski, 1991).

Five patterns of insular species distributions in presence-absence plots (random, minimum area, maximum isolation, block, and compensatory) have been proposed (Fig. 1) (Lomolino, 1986). Each pattern represents a biologically reasonable and testable hypothesis reflecting the effect of area and isolation on the distribution of a species, which aside from the random pattern, should reflect deterministic factors affecting variation in vagility and persistence ability of a species. A random pattern corresponds to a null hypothesis of 'no effect' of area or isolation on species distribution. A minimum area effect suggests a species' persistence on an island is limited below a threshold island size, but it has no constraints on dispersal within the archipelago. A species with relatively limited immigration abilities would exhibit a maximum isolation effect. A block pattern of species distribution arises when area and isolation operate together in an additive manner versus compensatory, where area and isolation interact to describe a diagonal pattern.

This species-based theory predicts that if non-random variation in species' characteristics influences persistence and vagility, then additive or compensatory patterns should be evident for some species within an archipelago and, when examined together, the distribution functions of the community should reflect the relative persistence and immigration abilities. Additionally, the compensatory pattern is expected to be more evident for archipelagos where the range of island area size and isolation is large relative to the persistence and dispersal abilities of the particular species. Support for the model is evident for some species in a few insular systems (Lomolino, 1986; 2000; see references therein); however, studies on a wide range of species across a variety of insular systems vary in their support for the model (Fritz, 1979; Adler & Wilson, 1985; Adler & Seamon, 1991; Lawlor, 1998; Peltonen & Hanski, 1991; Taylor, 1997; Wiggins & Møller, 1997; Watson *et al.*, 2005; Frick *et al.*, 2008; Presley & Willig, 2008).

Research on the influence of area and isolation on species incidence within archipelagos has focused on native vertebrates, but the principles of this species-based theory should apply to most organisms (Lomolino, 2000), including alien species. Alien species have been introduced globally, with rodents (e.g. *Rattus* spp. and *Mus musculus*) being some of the most widespread, invading over 80% of the worlds archipelagos (Atkinson, 1985; Atkinson & Towns, 2005; Innes, 2005b; Innes, 2005a; Towns *et al.*, 2006). Initially introduced to one or a few islands of an archipelago, alien rodents subsequently colonized other islands via human-aided mechanisms or unassisted dispersal (Russell *et al.*, 2008). Hypothetically, the factors of area and isolation that influence the dynamics of natural colonization and persistence should operate on the intra-archipelago immigration and extinction of alien populations. The extensive spatial, but brief temporal scale of these post-invasion colonizations by alien rodents provide an opportunity to further examine this species-based theory (Lomolino, 1986; 2000) without the confounding effects of evolutionary history (Harvey & Pagel, 1991) and enhance our understanding of the mechanical aspects of ecology, such as biogeographic processes (Sax *et al.*, 2005; Sax *et al.*, 2007).

The Galápagos Islands, Ecuador (Fig. 2) harbor three species of alien rodents for which the chronology and mechanisms of their initial introduction to the major islands of the archipelago are well understood (Patton *et al.*, 1975; Phillips *et al.*, in prep). Subsequently, additional populations of these three species have been established via dispersal within the archipelago from these "source" islands (see below; Phillips *et al.*, in prep); however, the dynamics of their intra-archipelago colonization of "satellite" islands remain unstudied. Our objective was to examine the influence of island area and isolation from source islands on the distribution of alien rodents on satellite islands in the archipelago within the framework of the species-based model (Lomolino, 1986; 2000). We hypothesized that isolation would have a lesser influence, compared to area, on the distribution patterns of alien rodents in the Galápagos Islands. Specifically, the close association of alien rodents with humans combined with a mobile human population should result in increased vagility and a reduced importance of immigration over persistence in the formation of species occurrences.

METHODS

Study area

The Galápagos archipelago includes approximately 129 islands and islets ranging in size from 0.02 to 458,812 ha (Fig. 2; Snell *et al.*, 1996; Phillips *et al.*, in prep). All islands are of volcanic origin with the highest reaching an elevation of 1700 m. Climate is strongly affected by ocean currents resulting in a warm (January – May) and a cool season (June – December). From 1965-2004, temperatures on Santa Cruz Island in the arid zone ranged from 22.6 to 26.2°C with an annual mean of 23.95°C±0.14 SE (Snell & Rea, 1999; 2000; unpublished data from the Charles Darwin Research Station). Precipitation varies considerably with season and elevation. During the warm season, rainfall generally occurs at all elevations, while in the cool season the highlands are characterized by persistent light rains and mist with the lowlands markedly dry. From 1965-2004, rainfall in the arid zone of Santa Cruz averaged 491.44 mm with a median of 277.55 mm (due to high annual variation). The vegetation is characterized by seven distinct zones along an elevation gradient. Increasing from sea level the zones are: littoral (coastal), arid, transitional, *Scalesia*, zanthoxylum (brown), Miconia, and pampa (fern-sedge). Only the larger islands have all vegetations zones, whereas the vegetation on the smaller islands and islets is comprised entirely of littoral zone. Most of the land area (> 95%) is protected as the Galápagos National Park (GNP) with the remainder urban and agricultural. Five islands are permanently occupied by humans though many others are visited frequently by tourists and fishermen.

Source island rodent invasion history

Black rats (*Rattus rattus*) first colonized Santiago in the 1600s (Patton *et al.*, 1975). In a second wave of introductions, black rats colonized Floreana, San Cristóbal, and Isabela in the mid-to late 1800s. Pinzón was also colonized in the 1800s, but it is unclear if this represents a unique introduction, separate from the aforementioned second wave. Finally, black rats were introduced to Santa Cruz and Baltra in the 1930s and 1940s. Aside from Pinzón, all of the above islands are currently or were previously (Santiago) inhabited by humans. House mice (*Mus musculus*) were first recorded in 1899, but are thought to have arrived in the 1600s (Phillips *et al.*, in prep). They co-occur with black rats on all the above islands except Pinzón. Santa Cruz and San Cristóbal are the only source islands on which Norway rats (*R. norvegicus*) are found, having arrived in the mid-1980s (Phillips *et al.*, in prep).

Rodent presence/absence data collection

We obtained presence/absence data for alien rodents in the Galápagos from two sources: records from earlier researchers (see review in Phillips *et al.*, in prep) and our own field work. The majority of the data was collected by the authors during field surveys from 1997-2003. Surveys of islands, other than Santa Cruz, where we were based, were made via boat. On most trips, research teams worked ashore, but lived aboard ship. On a few occasions, after transport to an island, teams made base camps on the interior and conducted field work from there. We conducted surveys at all times of the year and followed one of two procedures. When we were able to visit locations on consecutive days we placed live traps using either 41 x 13 x 13 cm Tomahawk traps in combination with 23 x 7.5 x 9 cm Sherman traps, or Sherman traps alone. We placed traps on transects spaced at 25 m as terrain would allow. Transect length and number of traps varied according to island size. On trips when we were unable to remain on site overnight, we placed rodent bait stations of 30 x 7 cm open-ended polyvinyl chloride (PVC) tubes (Catling *et al.*, 1997; Lindenmayer *et al.*, 1999). In addition to the bait, we placed double-sided tape inside tubes to aid in the collection of rodent hair. Bait stations were place on transects in a pattern similar to that used with the traps. If rodent presence was indicated (e.g. hairs, feces, tracks), we returned to the island to place traps to confirm the species identity.

Statistical analysis

From the patterns proposed by Lomolino (1986), we developed five *a priori* models for each species of alien rodent to explain their distribution on satellite islands in the Galápagos (Table 1). Similarly, we examined separately the distribution of black rats on satellite islands near their respective source islands (Table 1). Sample sizes for house mice and Norway rats were insufficient to perform a similar analysis. Because of the dichotomous nature of our response variable, rodent presence (1) or absence (0), we used binary logistic regression to assess the influence of the explanatory variables, area and isolation, on a species' probability of occurrence (Rita & Ranta, 1993; Hosmer & Lemeshow, 2000). Islands where rodents were confirmed, but later were eradicated or went extinct, are designated as having rodent presence in the analyses. We obtained area values for islands from Snell *et al*. (1996). We defined isolation as the shortest over-water distance incorporating any potential stepping stone islands from the nearest source island. We calculated distances using OpenEV, FWTools 2.4.2 (http://fwtools.maptools.org) shortest straight line distance from the nearest source island. Because immigration rates can vary greatly with shore geometry (Taylor, 1987), we excluded from the analyses five islands (Beagle Crater Islets1-5) located in a brackish lake on Isabela. The distribution of island area was right skewed with only six of the islands analyzed larger than 500 ha, whereas, the ranges of island distances from source were more evenly distributed. Though not required for logistic regression, we log-transformed area and distance to normalize their distributions, which should yield more stable solutions (Hosmer & Lemeshow, 2000). We assessed the collinearity of area and isolation for each of the separate analyses using Pearson's r (Hosmer & Lemeshow, 2000). Collinearity for the separate analyses was moderate, ranging from $r = 0.376$ to 0.585, which we evaluated by examining estimated standard errors and coefficients (Hosmer & Lemeshow, 2000). In the compensatory models, we mean-centered the interaction and main effect terms to improve interpretability of coefficients in the regression equation (Aiken & West, 1991). The fit of each model was assessed using the Hosmer and Lemeshow χ^2 goodness of fit test (Hosmer

& Lemeshow, 2000). We used SPSS Version 16.0 for logistic regression analyses unless otherwise stated.

We compared the five models for each species of rodent using the AIC (Akaike's Information Criterion; Burnham & Anderson, 2002) and adjusted for small sample size (n / K < 40) using the second-order form:

$$\mathrm{AIC_c} = -2log_e(L) + 2K + \frac{2K(K+1)}{n-K-1}$$

where $-2log_e(L)$ is the value of the maximized-log-likelihood of the model reflecting overall fit of the model, K is the number of estimable parameters in the model (i.e., the number of explanatory variables + 1, to include the intercept), and n is the number of observations (islands), which for all species equals 81. The $\mathrm{AIC_c}$ penalizes models for addition of parameters thus balancing explanatory power and parsimony (Burnham & Anderson, 2002). We ranked the models by $\mathrm{AIC_c}$ value with the lowest value considered the "best" model of those specified. We then compared models using two measures: $\Delta\mathrm{AIC_c}$ and Akaike weights (w_i; Burnham & Anderson, 2002). The $\Delta\mathrm{AIC_c}$ is simply a measure of each model relative to the best model, calculated as $\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{min}$. Models with $\Delta_i < 2$ indicate substantial support. Those with Δ_i between 3 and 7 suggest considerably less support, whereas those with $\Delta_i > 10$ have essentially no support (Burnham & Anderson, 2002). The w_i provides evidence for a model relative to the entire candidate set of R models and calculated as:

$$w_i = \frac{\exp\left(-\frac{\Delta_i}{2}\right)}{\sum_{r=1}^{R} exp\left(-\frac{\Delta_r}{2}\right)}$$

This changes the scale of the Δ_is rescaling them relative to 1 making w_i equivalent to the probability of a model being the best among the set of models.

If no single model was clearly best (wi ≥ 0.90; Burnham & Anderson, 2002), we selected a “confidence set” of models as those with a w_i within 10% of the highest (Royall, 1997). From the confidence set, we obtained model averaged estimates of parameter coefficients (Royall, 1997; Burnham & Anderson, 2002). We calculated estimates using the form:

$$\hat{\bar{\theta}} = \sum_{i=1}^{R} w_i \, \hat{\theta}_i$$

where $\hat{\theta}$ is the estimated parameter coefficient for the variable in the i model. When a specific model did not include a given parameter, the value of the coefficient was set at 0. For each model average, we calculated the precision (SE) of the parameter estimate using:

$$\text{SE} = \sum_{i=1}^{R} w_i \sqrt{(\hat{\theta}_i | g_i) + \left(\hat{\theta}_i - \hat{\bar{\theta}}\right)^2}$$

where g_i is a given model. Using the parameter coefficients from the selected best model or the model-averaged estimates, we developed graphical models showing the relationship of area and isolation on probability of occurrence for alien rodents. Finally, to assess the relative importance of individual predictor variables, we summed the w_i for all models within the confidence set containing a given predictor variable (Burnham & Anderson, 2002).

RESULTS

Black rats were the most widespread species occurring on 26 of the 81 satellite islands analyzed (Fig. 3a), whereas house mice were recorded on 4 islands (Fig. 3b). Norway rats were found on only one island (Fig. 3c), which precluded our fitting a logistic regression model for this species. Logistic regression models were fit for black rats and house mice

(Table 1). Black rats showed a compensatory pattern of distribution (Fig. 3a) where the relationship between the probability of occurrence and the degree of isolation was dependent on island size. Model selection results supported this relationship with the compensatory model being the best with an Akaike weight, $w_i = 0.956$ (Table 1). House mice displayed a similar compensatory pattern of distribution (Fig. 3b). Model selection revealed the null model as the best model, though there was substantial support for all the candidate models with their AIC_c values differing by < 2 (Table 1). Examined individually, area and isolation were of relatively equal importance in their effect on the distribution of both black rats and house mice (Table 2); however, the magnitude of the effect of each factor was much greater in black rats.

By examining the patterns of distribution of black rats from the colonization periods, we were able to obtain sufficient data for logistic regression analysis for four of the seven source islands: Santiago, Isabela, Santa Cruz, and Baltra (Table 1). Because of the close proximity of Santa Cruz and Baltra, their similar invasion history, and the fact that Baltra has only three satellite islands, we pooled data from these two islands for the analysis. Black rats on satellite islands of Santiago displayed a pattern of distribution intermediate between additive and compensatory (Fig. 4a). The additive model best fit the data (Table 1), but the compensatory model was strongly supported ($\Delta_i = 1.220$), indicating area and isolation both influence the distribution of rats, but that the interactive effect was weaker than the additive effect. The distribution of black rats on satellite islands of Isabela showed a pattern of maximum isolation (Fig. 4b) and was supported by results from model selection (Table 1). The logistic regression analysis revealed a situation of “complete separation” where isolation completely predicted the incidence of rats (So, 1995; McCarthy, 2007). When this occurs, the maximum likelihood estimate (MLE) does not exist and the log-likelihood becomes 0. Results for the additive and compensatory models were not presented because the MLE did not exist for any model that included the isolation term. On the satellite islands of Santa Cruz and Baltra, black rats showed a compensatory pattern of distribution where the relationship between the probability of occurrence and island size was dependent on the degree of isolation (Fig. 4c); however, the compensatory model did not have substantial support (Δ_i = 2.957) (Table 1). Instead, the additive model was best with the isolation only model having strong support (Δ_i = 0.034). Examined individually, area and isolation were of relatively equal importance in explaining the distribution pattern of rats on Santiago's satellites (Table 2). On Isabela's satellites the distribution pattern of rats was explained by isolation alone, whereas on satellites of Santa Cruz and Baltra, area was important in describing the distribution pattern of rats, although secondary to isolation.

Parameter estimates for isolation were negative for all analyses and positive for area for all but Isabela (Table 3). This indicated that as distance from the source island increases, the probability of a rodent occurring on an island decreases and as island size increases, the probability of rodent occurrence increases (Fig. 5). Incidence functions for black rats archipelago wide revealed the likelihood of a rat occurring on an island 0.02 ha or smaller was essentially zero, regardless of isolation (Fig. 5a). For islands 0.1 ha, the probability of a rat occurring on an island was dependent on the interaction of area and isolation and for islands larger than 0.1 ha isolation appears to be the determinant factor. The probability of house mice occupying an island was low overall (Fig. 5b) exceeding 50% only on islands ≥ 100 ha and within approximately 6 m of the source island. However, the precision of the estimates for house mice are likely low since only four of the 81 islands were occupied, which limits the predictive ability of the model. Incidence functions for satellite islands off Santiago and Santa Cruz and Baltra indicate the probability of a black rat occurring on an island of any size was greater than 50% if within 3,200 m or 17,000 m, respectively, of the source island (Fig. 5c,d). Wide confidence intervals for analyses of black rats on satellite islands were most likely due to the small sample sizes. Because the MLE did not exist for Isabela (see above), no parameter estimates were generated. We attempted to obtain parameter estimates using an exact inferential procedures test using R Version 2.9.1 and SAS Version 9.1(Cox, 1970; Hirji *et al.*, 1987; Zamar *et al.*, 2007). Estimates for area and isolation were generated, but results for the intercept were degenerate (Derr, 2000), precluding the calculation of an incident function for Isabela.

DISCUSSION

We extended a species-based model (Lomolino, 1986) to examine the influence of area and isolation on the intra-archipelago distribution of alien rodents. In the Galápagos Islands, black rats and house mice both show a compensatory pattern of distribution (Fig. 3a,b), which was strongly supported by regression analyses for black rats, but less so for house mice (Table 1). This suggests the combined processes of immigration and extinction are structuring incidence patterns for alien rodents (Lomolino, 1986; 2000), such that species have a high incidence on islands if low immigration rates are compensated for by low extinction rates or high immigration rates compensate for high extinction rates. The prevalence of the compensatory pattern in the Galápagos Islands may be attributable to the extensive geographic range over which the analyses were conducted (Lomolino, 1986), which covered six orders of magnitude for area (0.02 – 64248.00 ha) and almost five for distance (8 – 181,083 m; Fig. 3). An equally large scale of analysis of the distribution of native small mammals on islands in Massachusetts, USA, found no evidence of an interaction between area and isolation or additive effect (Adler & Wilson, 1985). At our smaller scale analysis of black rat distribution on satellite islands, a compensatory pattern was evident, but much weaker (Fig. 4a,c). It is unlikely the positive correlation of island area with distance contributed significantly to the observed compensatory pattern. Parameter estimates and standard errors generally were not inflated and the highest correlation of area and isolation was for Isabela (*r* = 0.585). This analysis revealed a maximum isolation effect, whereas the lowest correlation was for Santa Cruz and Baltra (*r* = 0.376), which showed support for a compensatory pattern.

While area was an important factor in additive and compensatory models explaining the distribution of black rats, area alone ranked low in all models. This suggests that the minimum threshold island size in the Galápagos Islands on which rats can persist without benefit of a "rescue effect" (Brown & Kodric-Brown, 1977) is very low, perhaps below 0.1 ha (Figs. 4b & 5a). To persist on islands elsewhere, black rats appear to require islands larger than in the Galápagos (Howald *et al.*, 2007; but see Lee, 1999; Lorvelec & Pascal, 2005). Minimum area thresholds for at least some species of native rodents (*Clethrionomys gapperi, Peromyscus leucopus, P. maniculatus, Zapus hudsonius*) are considerably larger (0.3 – 4 ha), despite having body sizes less than half that of black rats (Foster, 1965; Crowell, 1973; Adler & Wilson, 1985). All factors being equal, ecological theory would predict higher overall resource requirements for larger bodied black rats and larger islands to support a population (Nagy, 1987). The ability of black rats to persist on small islands in the Galápagos archipelago could result from two mechanisms. First, tolerance for high population densities may provide a buffer from demographic stochasticity leading to extinction (Crowell, 1973; Lott, 1984). Secondly, black rats may be able to sustain population sizes sufficient to avoid extinction on relatively small, habitat-poor islands due to marine inputs subsidizing the limited resources in the terrestrial system (Stapp & Polis, 2003b; 2003a).

In contrast to area, isolation ranked high in all models describing the distribution of black rats (Table 1) and was the predominant factor at the satellite island level (Table 2). In the Galápagos Islands, immigration ability appears to have limited black rat dispersal beyond 1239 m (Fig. 4a). Similarly, in Australia and New Zealand, black rats are known to have crossed sea channels up to 1.4 km and 1 km, respectively (Burbidge, 2004; Russell *et al.*, 2008). It is noteworthy that the maximum dispersal distance by black rats in the Galápagos Islands occurs on satellites of Santiago, the island first invaded in the early 1600s (Patton *et al.*, 1975). Maximum dispersal distances from Isabela, invaded in the mid-to late 1800s, and from Santa Cruz and Baltra, invaded in the 1930s and 1940s, are 831 m and 924 m, respectively. The average distance from source for occupied satellite islands reveals a similar pattern (Santiago $\bar{X} =$ 611 m, Isabela $\bar{X} =$ 524 m, Santa Cruz & Baltra $\bar{X} =$ 242 m). These data suggest that the immigration and extinction processes on Santiago's satellites may have reached an equilibrium, whereas on the satellites of Isabela and Santa Cruz and Baltra these processes are in an early and more dynamic stage with the potential for black rats to reach more distant islands in the future. The absence of area as a factor in describing black rat distribution on Isabela may be an artifact arising from characteristics unique to Isabela's satellite islands (i.e., absence of islands closer than 200 m) or possibly due to inadequate sampling.

Although house mice occur on only four islands, it is unclear if poor vagility limits their distribution in the Galápagos. In Australia, mice crossed open-water channels of approximately 500 m (Burbidge, 2004) making at least 32 islands in the Galápagos Islands within their immigration capacity. Whereas, in New Zealand human transport is assumed to be the principal dispersal mechanism of house mice (Taylor, 1975). Extinction, driven by inter-specific interference competition with black rats (Choquenot & Ruscoe, 2000; Ruscoe, 2001; Caut *et al.*, 2007), may be the principal cause of their absence from islands. On Plaza Sur and Norte, where mice currently occur, black rats are absent. On the two other islands where mice are reported (Seymour and Mosquera), they were detected during the same sampling period with black rats (Key & Muñoz Heredia, 1994). Subsequent surveys have failed to detect house mice on these two islands, suggesting black rats were a factor in their extinction. Less correlative evidence from Santiago indicates house mice exhibit "competitive release" in response to removal of black rats (Harris & Macdonald, 2007) and outside of the Galápagos, house mice numerically increase following the eradication of black rats (Innes *et al.*, 1995; Murphy *et al.*, 1999). Although inter-specific competition may be the proximate cause of the limited distribution of house mice, the low habitat diversity and lack of refugia may be the ultimate cause as house mice and black rats are sympatric on six large islands in the Galápagos archipelago.

The limitation of Norway rats to a single satellite island not only precludes any quantitative analysis, it is perplexing as their swimming abilities surpass those of black rats (Russell *et al.*, 2008); however, their presence on Rabida, more than 24 km from a source island, must be human-facilitated. The failure of Norway rats to disperse across the Galápagos archipelago may result from interspecific interactions. In the Seychelles, Norway and black rats do not co-occur on any islands (Hill *et al.*, 2003) and in New Zealand, the probability that Norway rats will occur on an island is lower if another alien rodent is present (Yom-Tov *et al.*, 1999; Russell & Clout, 2004). Despite being larger than black rats and the dominant species in enclosure experiments (Barnett & Spencer, 1951; McCartney & Marks, 1973) Norway rats are competitively inferior in some environments (Atkinson, 1986; Yom-Tov *et al.*, 1999). In the Galápagos Islands, black rat superiority may arise from the "priority effect" conveying an advantage to the species arriving first (Lockwood *et al.*, 1999). Niche requirements of Norway rats may contribute to their low incidence on islands in the Galápagos. In New Zealand, Norway rats are habitat specialists, compared to black rats, preferring wetland habitats (Moors, 1990). After the initial invasion on Santa Cruz, Norway rats rapidly (10 to 12 years) expanded their range 16 km into the islands' mesic highlands (Key & Muñoz Heredia, 1994). Surveys in the early 2000s revealed Norway rats had not appreciably expanded their range beyond the central highlands and were largely absent from xeric habitats (i.e., littoral, arid, and transitional zones) including most of eastern, western, and northern Santa Cruz (Phillips *et al.*, in prep). This suggests Norway rats are not well adapted to colonizing Galápagos' arid off-shore islands. Although it is unclear to what extent black rats exclude them.

We show that this species-based model (Lomolino, 1986) can be used to explain alien rodent distributions in insular systems. Our results for black rats support the model's prediction (Lomolino, 1986; 2000) that immigration and extinction operate simultaneously, in an additive or compensatory manner, to determine the distribution of insular species. Our research also suggests mechanisms not directly related to vagility and persistence, such as incumbent advantage (Russell & Clout, 2004), habitat preferences (Moors, 1990), and interspecific interactions (Caut *et al.*, 2007) may have an equally influential effect on insular distributions of rodents. We refuted our hypothesis that alien rodent commensalism would increase the vagility of rodents and reduce the importance of island isolation in structuring incidence functions. It is possible other biotic and abiotic factors influence the distribution of alien rodents in the Galápagos. Further analysis at a more detailed level is warranted to define and understand the mechanisms driving intra-archipelago invasion of alien rodents.

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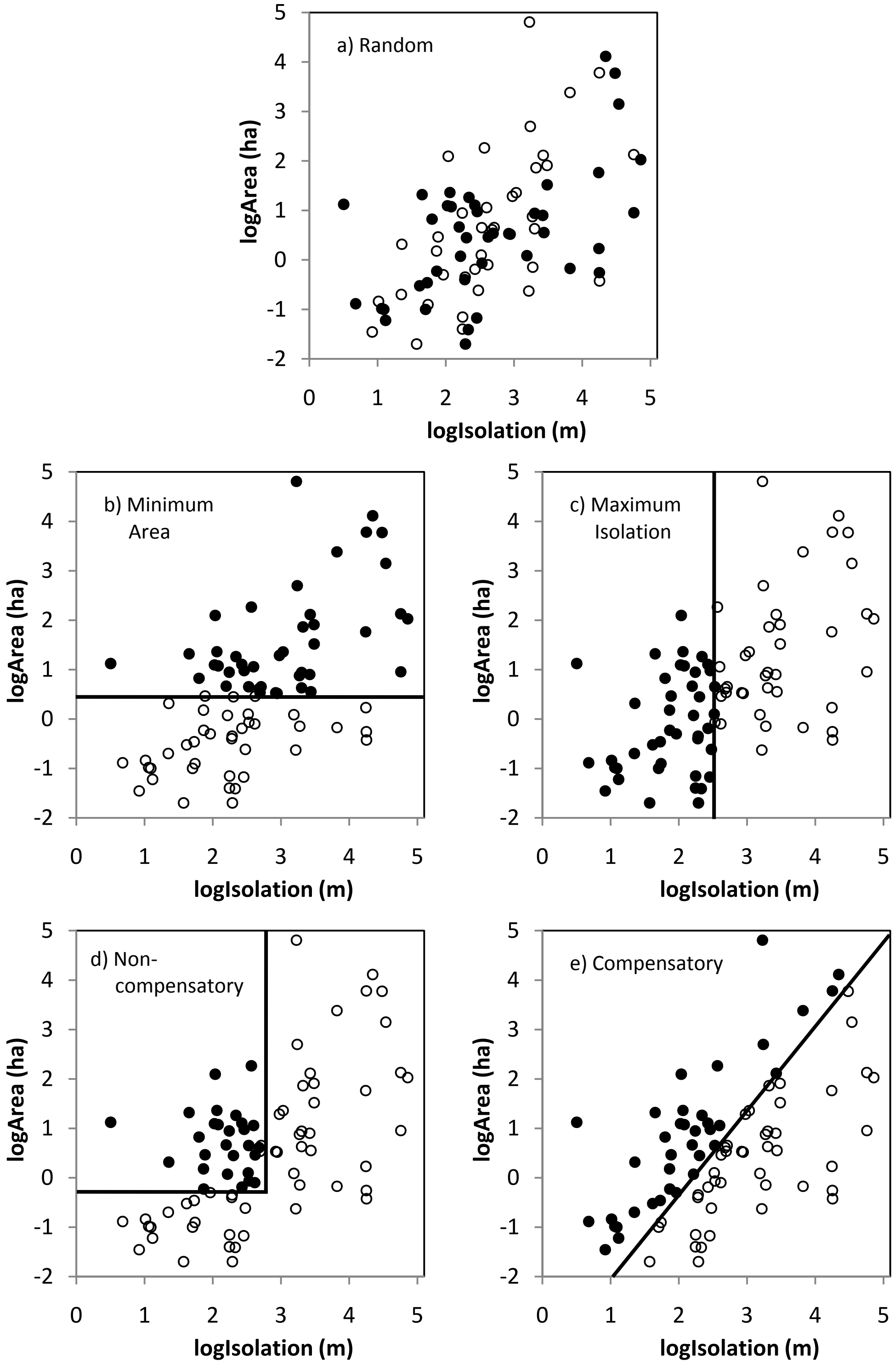

Figure 1 Hypothetical species occurrence patterns (after Lomolino 1986) on the 81 sampled satellite islands in the Galápagos archipelago. Presence is indicated by closed circles, absence by open circles. See text for theoretical basis for each pattern. Note circles represent real islands, but patterns do not represent actual distributions.

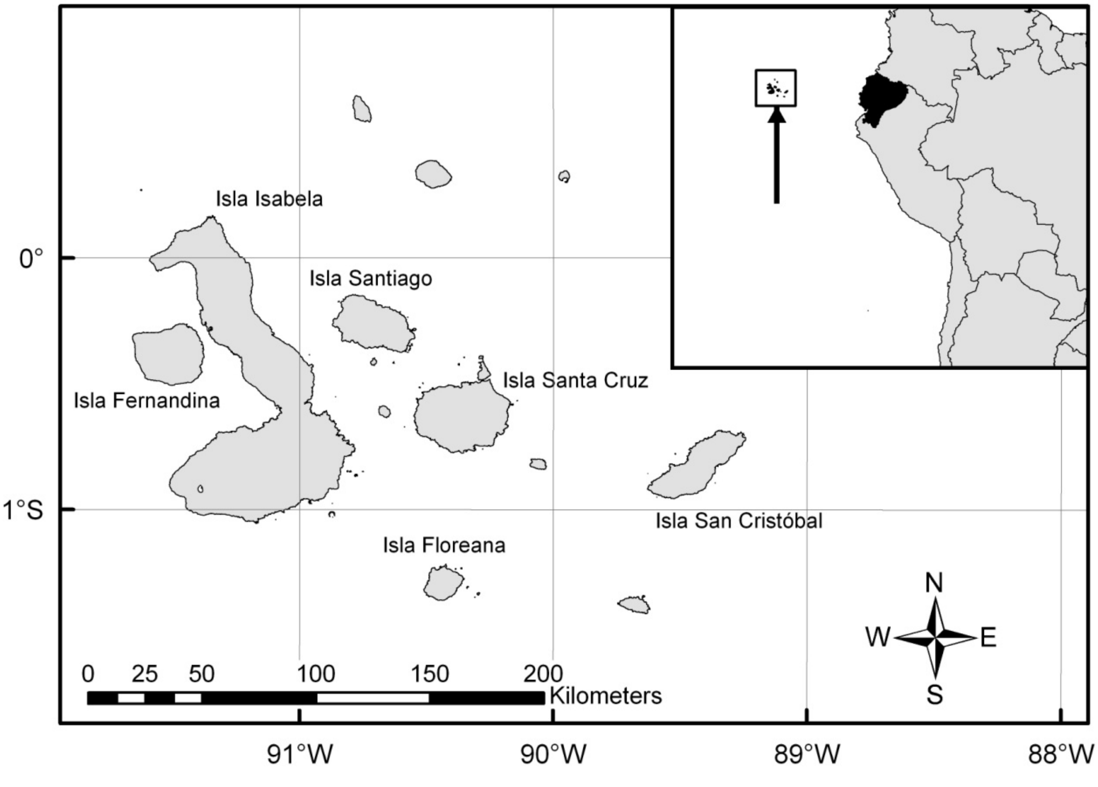

Figure 2 The Galápagos archipelago of Ecuador and its location relative to South America.

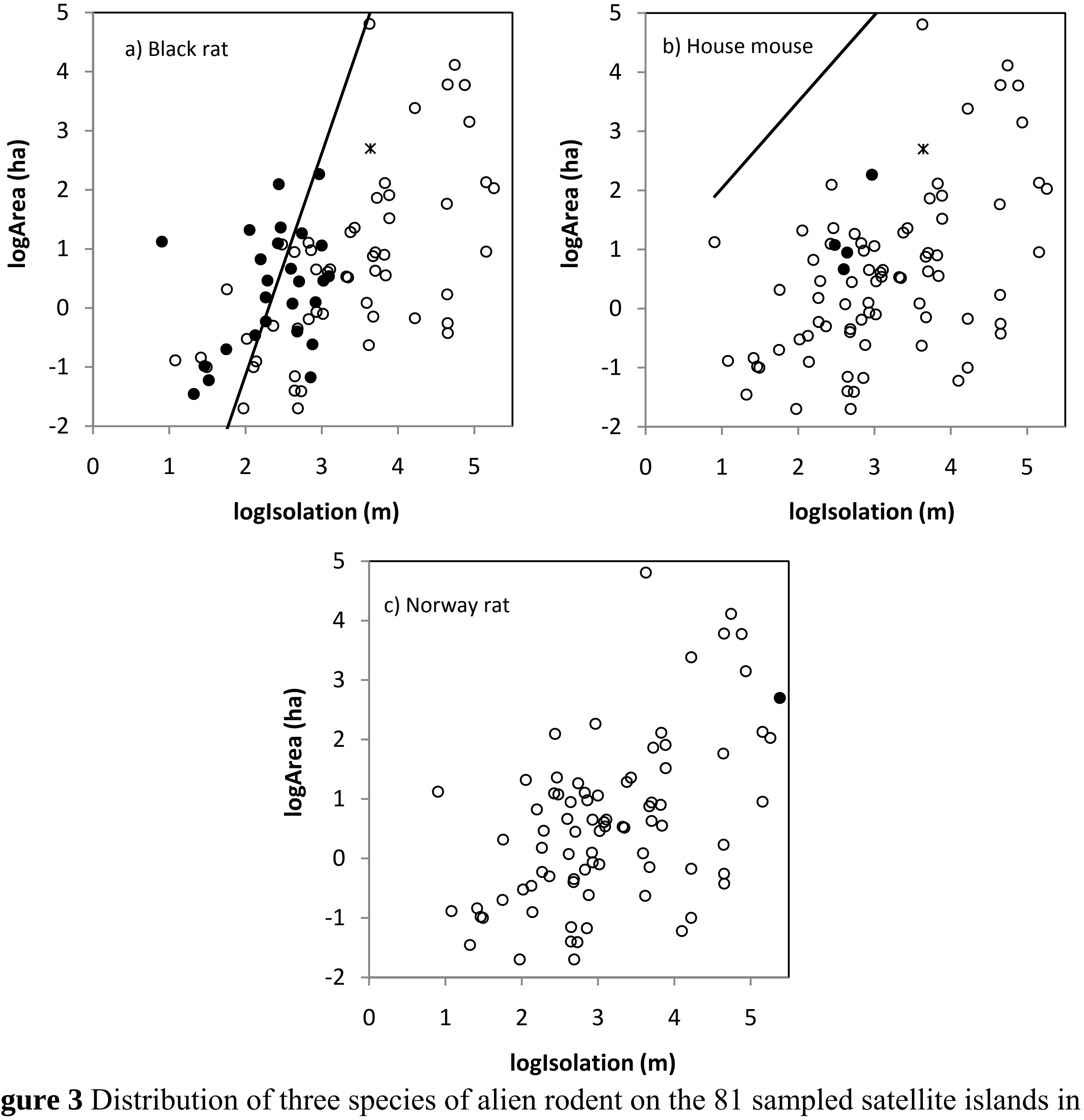

Figure 3 Distribution of three species of alien rodent on the 81 sampled satellite islands in the Galápagos archipelago. Presence is indicated by closed circles, absence by open circles. Lines represent the threshold above which the probability of occurrence is > 50%. Lines were derived using the logistic regression equation, following Rita and Ranta (1993). Source distance for island occupied by Norway rats (Rabida) is greater than source distance for black rats and house mice (*).

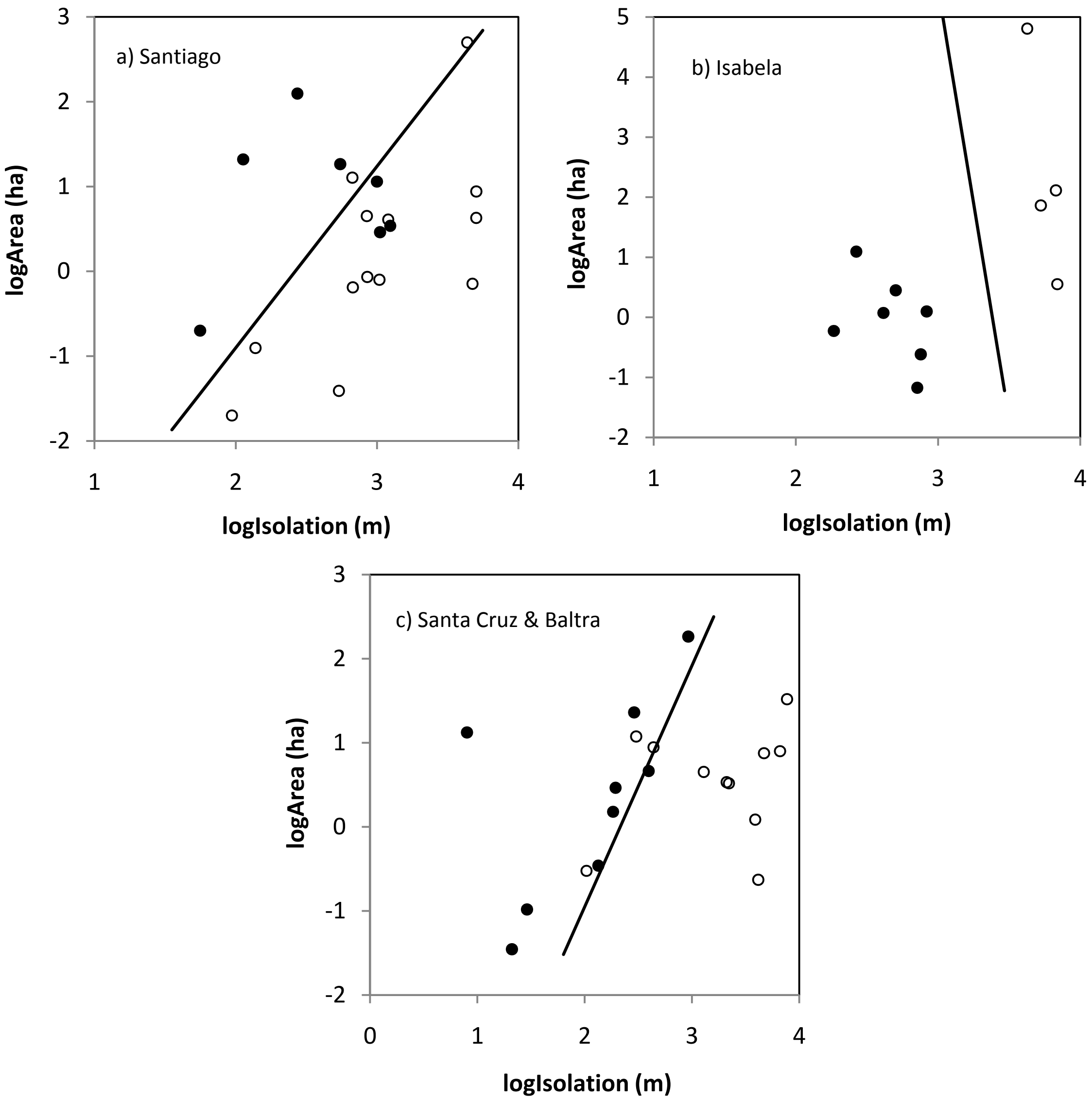

Figure 4 Distribution of black rats on the satellite islands off their presumed source island in the Galápagos archipelago. Each distribution represents a distinct period of introduction of black rats in the Galápagos: a) late 1600s to early 1700s, b) early to late 1800s, and c) 1930s to 1940s (see text; Patton et al. 1975). Presence is indicated by closed circles, absence by open circles. Lines represent the threshold above which the probability of occurrence is > 50%. Lines were derived using the logistic regression equation, following Rita and Ranta (1993). Insufficient sample sizes precluded analysis of three source islands: Floreana, Pinzón, and San Cristóbal.

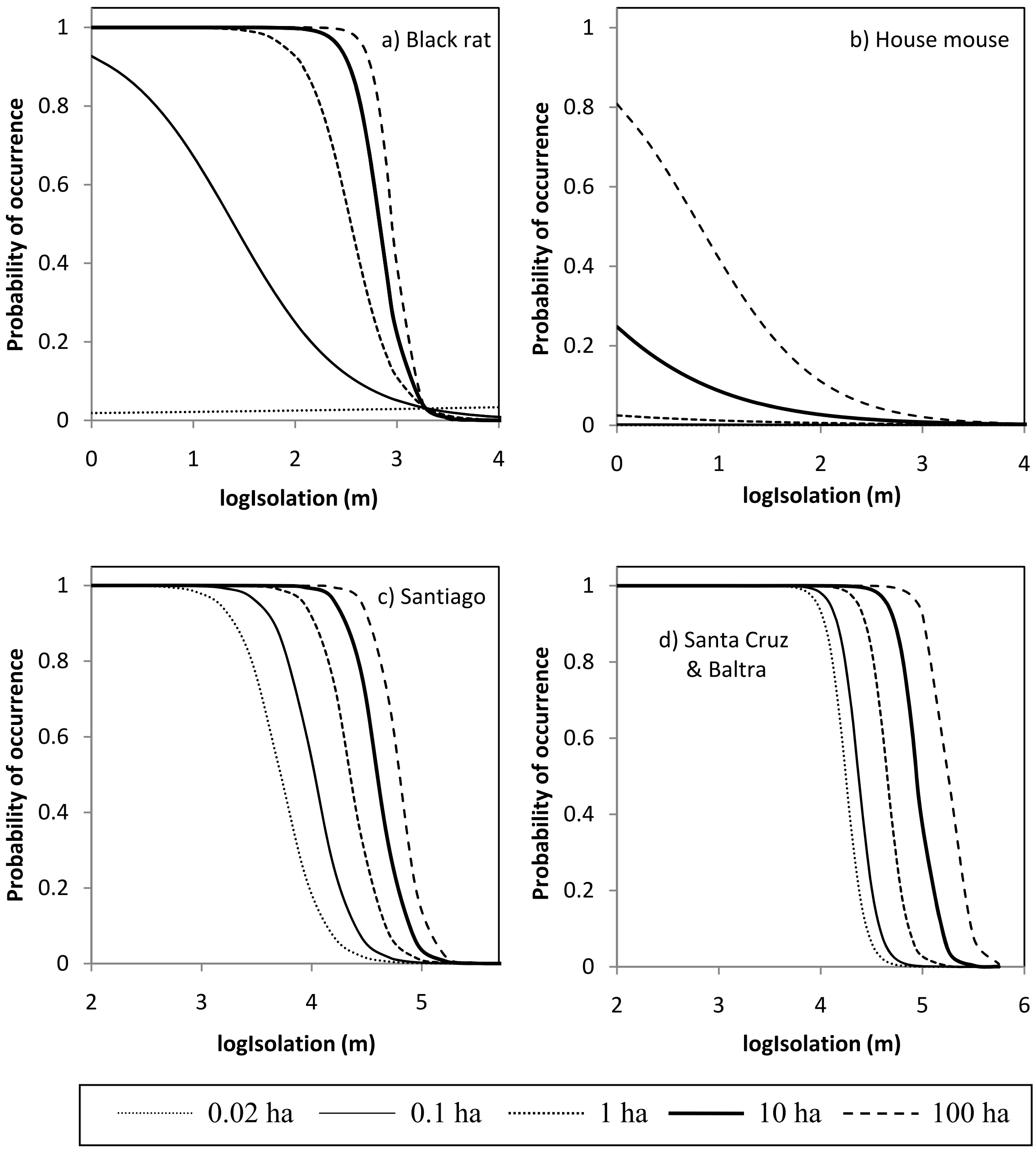

Fig. 5 Incidence functions showing the effect area and isolation on the probability of occurrence of black rats and house mice on the 81 sampled satellite islands in the Galápagos archipelago and black rats on the satellite islands off two presumed source islands. Coefficients for b-d) were derived from model-averaged parameter estimates. Minimum island area was 0.02 ha for all analyses, except d).

Table 1 Model selection results from logistic regression analyses on the occurrence of two alien rodents on the 81 sampled satellite islands in the Galápagos archipelago and of black rats on the satellite islands off three presumed source islands. The three islands have distinct periods of introduction for black rats (see text). Models are derived from five *a priori* hypotheses (after Lomolino 1986) and are ranked by AIC_c. K is the number of parameters in a model, including the intercept, $log_e(L)$ is the value of the maximized-log-likelihood, Δ_i is the difference between the best model and a given model, and w_i is the Akaike weight.

Species / Island	Model	K	$-2 \times log_e(L)$	AIC_c	Δ_i	w_i
Black rat	Area × isolation	4	68.258	76.784	0.000	0.956
	Area + isolation	3	77.489	83.801	7.016	0.029
	Isolation	2	80.860	85.014	8.230	0.016
	Null	1	101.673	103.724	26.939	0.000
	Area	2	100.128	104.282	27.498	0.000
House mouse	Null	1	31.864	33.915	0.000	0.266
	Area × isolation	4	25.586	34.112	0.198	0.241
	Area + isolation	3	28.081	34.393	0.478	0.209
	Area	2	30.996	35.150	1.235	0.143
	Isolation	2	31.020	35.174	1.259	0.142
Santiago	Area + isolation	3	16.692	24.192	0.000	0.511
	Area × isolation	4	14.745	25.412	1.220	0.277
	Isolation	2	23.125	27.831	3.639	0.083
	Null	1	25.898	28.120	3.928	0.072
	Area	2	23.847	28.553	4.361	0.058
Isabela*	Isolation	2	0.000	5.500	0.000	0.943
	Area	2	5.710	11.210	5.710	0.054
	Null	1	14.421	16.865	11.365	0.003
Santa Cruz	Area + isolation	3	12.208	19.708	0.000	0.450
	Isolation	2	15.036	19.742	0.034	0.443
	Area × isolation	4	11.998	22.665	2.957	0.103
	Null	1	27.526	29.748	10.040	0.003
	Area	2	27.296	32.002	12.294	0.001

* Additive and compensatory models are omitted (see text).

Table 2 Relative importance of the explanatory variables (area and isolation) among the candidate models for each species or satellite island group. Values are the sum of Akaike weights (w_i) within the confidence set of models containing the given variable.

Species / Island	Area	Isolation
Black rat	0.984	1.000
House mouse	0.593	0.591
Santiago	0.846	0.871
Isabela	0.054	0.943
Santa Cruz	0.554	0.996

Table 3 Parameter estimates from logistic regression analyses and 95% confidence intervals in parentheses for the effect of area, isolation, and interaction term on the incidence of black rats and house mice on the 81 sampled satellite islands in the Galápagos archipelago and of black rats on the satellite islands of three presumed source islands in the Galápagos.

Species / Island	β_0 (intercept)	β_1 (logArea)	β_2 (logIsolation)	β_3 (logArea×logIsolation)
Black rat	-0.85 (-1.60, -0.10)	0.29 (-0.52, 1.11)	-2.72 (-4.22, -1.22)	-1.22 (-2.32, -0.12)
House mouse*	-2.31 (-5.20, 0.58)	0.42 (-0.26, 1.10)	-0.45 (-1.35, 0.46)	-0.23 (-0.72, 0.27)
Santiago*	4.52 (-7.18, 16.23)	1.43 (-0.37, 3.23)	-3.23 (-7.20, 0.74)	-0.44 (-1.52, 0.64)
Isabela†	na	-2.36 (-7.71, -0.25)	-3.92 (-∞, -1.07)	na
Santa Cruz*	9.32 (-5.03, 23.67)	1.11 (-0.96, 3.18)	-4.45 (-10.59, 1.68)	0.09 (-0.40, 0.58)

* Parameter estimates and confidence intervals were derived using model averaging.

† Parameter estimates were derived from the sufficient statistic using exact inference.

CHAPTER 3

MODELING THE INTRA-ARCHIPELAGO DISTRIBUTION OF ALIEN RODENTS IN THE GALÁPAGOS ISLANDS: CONSERVATION IMPLICATIONS AND APPLICATIONS

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ABSTRACT

Alien rodents (*Rattus* spp. and *Mus musculus*) are among the most devastating invasive species for insular flora and fauna. Our goal was to identify the factors that correlate with the distribution of two species of alien rodents, black rats (*Rattus rattus*) and house mice (*Mus musculus*), in the Galápagos Islands. We obtained presence/absence data for 81 islands in the archipelago. From a suite of 14 biotic and abiotic explanatory variables, we identified the factors to include in multivariate analyses. Using logistic regression we fitted models with the important variables and compared them using Akaike's Information Criterion (AIC). The presence of black rats on an island is influenced primarily by distance from a source population, with the probability of occurrence decreasing as distance from source increases. However, the effect of isolation is minimized by the presence of a stepping stone island or

increased visitation to the island by humans. Human visitation positively influences the occurrence of house mice on an island as do, to a lesser extent, the presence of predators and increasing island productivity. The occurrence of black rats on islands in the archipelago appears to be driven entirely by factors affecting their ability to immigrate to an island. Whereas, the incidence of house mice on an island is more complex involving an immigration related factor and biotic factors affecting persistence. Our results provide important information for biologists in the Galápagos working to prevent the spread of alien rodents within the archipelago.

INTRODUCTION

Alien rodents (*Rattus* spp. and *Mus musculus*) are among the most devastating invasive species for insular flora and fauna (Courchamp *et al.*, 2003; Towns *et al.*, 2006; Angel *et al.*, 2009). The magnitude of alien rodents' impact is due partially to the diverse ecological roles they occupy as potential competitors, predators, and herbivores (Courchamp *et al.*, 2003). Equally important is their ubiquity: this suite of species has been introduced to more than 80% of the world's archipelagos (Bronson, 1979; Atkinson, 1985). However, many islands within these archipelagos remain rat-free (Moors *et al.*, 1992), providing refugia for native flora and fauna (Sugiura *et al.*, 2009).

Widespread implementation of quarantine procedures have contributed to the decline in the rate of invasion by alien rodents to archipelagos and to islands within archipelagos (Atkinson, 1985; Russell *et al.*, 2008b). Concomitantly, conservation efforts have achieved remarkable success in eradicating alien rodents from increasingly larger islands allowing the recovery or repatriation of populations of native species (Courchamp *et al.*, 2003; Howald *et* *al.*, 2007). Despite these advances, reinvasion of islands cleared of alien rodents is a persistent threat, as is invasion of historically rodent-free islands (Thorsen *et al.*, 2000; Burbidge, 2004; Pitman *et al.*, 2005; Russell *et al.*, 2008b). Understanding the process of alien rodent invasion is fundamental to mitigating the threat they pose to native insular biota (Puth & Post, 2005; Russell *et al.*, 2009).

An invasion by an alien species consists of three phases: dispersal, establishment, and spread (Williamson, 1996; Kolar & Lodge, 2001; Leung *et al.*, 2002). From the perspective of preventing invasions by alien rodents, the dispersal phase is the most important to understand yet it is the least studied (Puth & Post, 2005). The anthropogenic pathways that facilitated the global spread of alien rodents to islands have been identified (Moors *et al.*, 1992; Mooney & Hobbs, 2002)as have the principal mechanisms that influence dispersal of native rodents to islands (Crowell, 1973; Adler & Wilson, 1985; Lomolino, 1986; Diamond, 1987). What is currently lacking is insight into the relative importance of these two processes (anthropogenic facilitation versus natural mechanisms) for intra-archipelago dispersal by alien rodents (Russell *et al.*, 2008a). For example, once an alien rodent becomes established on one island in an archipelago, is dispersal to other islands achieved via anthropogenic pathways, natural mechanisms, or both?

The ecological adaptability of alien rodents and their capacity to establish on islands in a variety of insular environments is evident from their global distribution (Atkinson, 1985; Jones *et al.*, 2008). However, some invasions by alien rodents fail to establish (Russell & Clout, 2005). Successful establishment of rodents on islands, both alien and native, is associated with several biotic and abiotic factors. Island area is often positively linked to rodent occurrence (Crowell, 1973; Adler & Wilson, 1985; Lomolino, 1986), but it is recognized that area *per se* is a correlate for other factors such as primary productivity or habitat diversity (Wright, 1983; Rosenzweig, 1995). The communities of predators and competitors (native or alien) can provide "biotic resistance" to invasion altering the probability of a species successfully establishing on an island (Baltz & Moyle, 1993; Crawley *et al.*, 1999; deRivera *et al.*, 2005). Alternatively, the presence and impact of non-native species may facilitate the invasion of other introduced species (Simberloff, 2006).

The Galápagos archipelago is comprised of several islands encompassing a wide range of island sizes and levels of isolation (Fig. 1; Snell *et al.*, 1996). The ecological integrity of the Galápagos archipelago is largely intact due to its relatively recent discovery and occupation by humans. Nevertheless, centuries of human activity and occupation in the archipelago have altered the landscape and degraded the system. Among the causes of degradation are many species of introduced plants and animals including alien rodents (see below; Patton *et al.*, 1975; Tye, 2006; Phillips *et al.*, in prep-a). The above features, in conjunction with the limited and controlled introduction pathways into the archipelago, make the Galápagos archipelago an ideal system to examine the process of intra-archipelago invasion by alien rodents.

Our objectives in this study were two-fold. First, we aimed to identify the biotic and abiotic factors associated with the presence and absence of alien rodents on "satellite" islands (see below) in the Galápagos archipelago and to determine if these factors differed between rodent species. Second, we attempted to develop a predictive model to determine the probability of an alien rodent occurring on or invading a satellite island in the archipelago. It is our hope that the results of this study will aid biologists in the development and application of management protocols for alien rodents in the Galápagos archipelago and elsewhere.

METHODS

The islands and the rodents

Straddling the equator and situated approximately 970 km west of Ecuador, the Galápagos archipelago is comprised of about 129 islands and islets (Fig. 1; Snell *et al.*, 1996; Phillips *et al.*, in prep-a). Islands range in size from small (0.02 ha) low-lying islets to large (458,812 ha) islands composed of active and dormant volcanoes, the highest reaching 1707 m a.s.l. Climate is characterized by a warm (January – May) and a cool season (June – December). Temperature and precipitation in the archipelago vary greatly with elevation, aspect, and season. From 1965-2004 (in the arid zone on Santa Cruz Island), temperature ranged from 22.6 to 26.2°C with the annual mean of 23.95°C±0.14 SE. During this time, rainfall averaged 491.44 mm (Snell & Rea, 1999; 2000). Seven vegetation zones are found in the islands (Wiggins & Porter, 1971). Increasing from sea level, the zones are: littoral (coastal), arid, transitional, *Scalesia*, zanthoxylum (brown), Miconia, and pampa (fern-sedge). Smaller, low-lying islands generally have only littoral zone vegetation, whereas only the largest islands possess all vegetation zones. Five of the larger islands are permanently occupied by humans; however, tourists and fishermen frequent most islands. Human settlement and agricultural areas comprise < 5% of the land area with the remainder protected as the Galápagos National Park (GNP).

Three species of alien rodent occur in the Galápagos archipelago. Black rats (*Rattus rattus*) arrived first (on Santiago island) in the 1600s (Patton *et al.*, 1975). During a second of introductions (in the mid-to late 1800s), black rats colonized Floreana, San Cristóbal, and Isabela islands. Pinzón was also colonized in the 1800s, but it is unclear if this represents a unique introduction separate from the aforementioned second wave. Finally, black rats were introduced to Santa Cruz and Baltra islands in the 1930s and 1940s. House mice (*Mus musculus*) are thought to have arrived in the 1600s, concurrent with black rats. However, the first record of their presence in the archipelago is from 1899 (Phillips *et al.*, in prep-a). They co-occur with black rats on all the above islands except Pinzón. Norway rats (*R. norvegicus*) are found on Santa Cruz and San Cristóbal islands and are thought to have arrived in the mid-1980s (Phillips *et al.*, in prep-a). All of the above islands, except Pinzón, are currently or were previously (Santiago island) inhabited by humans. We termed these seven islands (Baltra, Floreana, Isabela, Pinzón, San Cristóbal, Santa Cruz, and Santiago) "source" islands as their alien rodent invasion histories and pathways are relatively well-understood. We hypothesize that alien rodents disperse to "satellite" islands throughout the archipelago from these islands. At present, black rats and house mice are present on 26 and four satellite islands, respectively, whereas Norway rats are found on one (Phillips *et al.*, in prep-a).

Rodent and island datasets

Most presence/absence data for alien rodents were collected during field surveys conducted 1997-2003. We supplemented this data with records from earlier researchers (see review in Phillips *et al.*, in prep-a). We conducted surveys throughout the year and followed one of two procedures. When we were able to visit locations on consecutive days, we used live traps - either Tomahawk traps (41 x 13 x 13 cm) in combination with Sherman traps (23 x 7.5 x 9 cm) or Sherman traps alone. On sampling transects, traps were spaced at 25 m intervals (as terrain would allow). Transect length and number of traps varied according to island size. On trips when we were unable to remain on site overnight, we used rodent bait stations consisting of 30 x 7 cm open-ended polyvinyl chloride (PVC) tubes (Catling *et al.*, 1997;

Lindenmayer *et al.*, 1999). In addition to the bait, we placed double-sided tape inside tubes to aid in the collection of rodent hair. Bait stations were place on transects similar to traps. If rodent presence was indicated (e.g. hairs, feces, tracks), we returned to the island to place traps (method detailed above) to confirm the species identity. Islands where rodents were confirmed, but were later eradicated or went extinct, we designated as having rodents present in the analyses.

For each island in the study, we collected data on 14 explanatory variables (Table 1). Values for island area were obtained primarily from Snell *et al*. (1996) with additional data, including elevation and distance, calculated using OpenEV, FWTools 2.4.2 (http://fwtools.maptools.org). For island distance, we measured the shortest over-water path (m) from a source island incorporating stepping stone islands (MacArthur & Wilson, 1967) when this resulted in the shortest over-water distance. Because immigration rates can vary greatly with shore geometry (Taylor, 1987), we excluded from the analyses five islands (Beagle Crater Islets 1-5) located in a brackish lake on Isabela. As a proxy for above-ground net primary productivity on an island we used enhanced vegetation index (EVI) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS). For each island, we derived annual minimum, maximum and mean EVI values based on seven years of data. We used a time series of 155 images of the product referred to as MODIS 16-day vegetation index (MOD13Q1), which were obtained from the United States Geological Survey's Land Processes Distributed Active Archive Center (http://lpdaac.usgs.gov). All processing of satellite imagery was done with LDOPE Tools (Earth Resources Observation and Science Center, United States Geological Survey, Sioux Falls, South Dakota, USA) and ERDAS Imagine software (Version 9.1, Erdas Inc., Atlanta, Georgia, USA). Human population size estimates are for the latter part of the study period (González *et al.*, 2008). Data for human visitation and species variables (Table 1) were derived from Charles Darwin Research Station (CDRS) records. We log-transformed (base 10) the continuous variables to normalize their distributions.

Statistical analysis

We restricted our analyses of the distribution of alien rodents to black rats and house mice because Norway rats were confined to a single satellite island (Phillips *et al.*, in prep-b). We used binary logistic regression to examine the influence of the explanatory variables on a rodent species' probability of occurrence on an island (Hosmer & Lemeshow, 2000). To avoid overfitting of multivariate models, we first assessed the importance of each variable for a rodent species using univariate analyses. Variable importance was determined using the log-likelihood ratio test with $P < 0.25$ used as a cutoff for maintaining a variable (Mickey & Greenland, 1989). We assessed the multicollinearity of the remaining explanatory variables using Pearson's r (Hosmer & Lemeshow, 2000) and, in case of a strong correlation ($r > 0.75$), the variable with the lower P value was retained. Using the remaining variables for each species of rodent, we developed models using all possible variable combinations ($K^2 - 1$) and then performed multivariate analyses. Models were evaluated using the AIC (Akaike's Information Criterion; Burnham & Anderson, 2002). We adjusted for small sample size ($n / K < 40$) using the second-order form:

$$\mathrm{AIC_c} = -2log_e(L) + 2K + \frac{2K(K+1)}{n-K-1}$$

where $-2log_e(L)$ is the value of the maximized-log-likelihood of the model reflecting overall fit of the model, K is the number of estimable parameters in the model (i.e. the number of explanatory variables + 1 to include the intercept), and n is the number of observations (islands), which for all species is 81. We ranked the models by $\mathrm{AIC_c}$ value with the lowest value considered the "best" model of those specified. We then compared models using two measures: $\Delta\mathrm{AIC_c}$ and Akaike weights (w_i; Burnham & Anderson, 2002). The $\Delta\mathrm{AIC_c}$ is a measure of each model relative to the best model and is calculated as, $\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{min}$. Models with $\Delta_i < 2$ indicate substantial support, those with Δ_i between 3 and 7 suggest considerably less support, and those with $\Delta_i > 10$ have essentially no support (Burnham & Anderson, 2002). The w_i provides evidence for a model relative to the entire candidate set of R models and calculated as:

$$w_i = \frac{\exp\left(-\frac{\Delta_i}{2}\right)}{\sum_{r=1}^{R} exp\left(-\frac{\Delta_r}{2}\right)}$$

If no single model was clearly best ($w_i \geq 0.90$; Burnham & Anderson, 2002), we selected a "confidence set" of models (those with a wi within 10% of the highest; Royall, 1997). From the confidence set, we obtained model-averaged estimates of parameter coefficients (Burnham & Anderson, 2002). We calculated estimates using the form:

$$\hat{\bar{\theta}} = \sum_{i=1}^{R} w_i\, \hat{\theta}_i$$

where $\hat{\theta}$ is the estimated parameter coefficient for the variable in the i model. When a specific model did not include a given parameter, the value of the coefficient was set at 0. For each model average, we calculated the precision (SE) of the parameter estimate using:

$$\mathrm{SE} = \sum_{i=1}^{R} w_i \sqrt{\left(\hat{\theta}_i \middle| g_i\right) + \left(\hat{\theta}_i - \hat{\bar{\theta}}\right)^2}$$

where g_i is a given model. We developed graphical models showing the relationship of area and isolation on probability of occurrence for alien rodents using the parameter coefficients from the model-averaged estimates. We summed the w_i for all models within the confidence set containing a given predictor variable to assess the relative importance of individual predictor variables (Burnham & Anderson, 2002). High AIC_c weight and model-averaged estimates that are greater than their standard errors characterize important variables (Anderson, 2008).

We presented the coefficient of determination, R^2_N, (Nagelkerke, 1991) for all candidate models to evaluate their overall fit to the data. We calculated the receiver operating characteristic (ROC) curve to evaluate the predictive accuracy of a model (Zweig & Campbell, 1993; Fielding & Bell, 1997). In the ROC curve, the proportion of correctly predicted occupied islands (sensitivity) is plotted against 1 minus the proportion of correctly predicted absences (1-specificity). A ROC curve yielding a 45° line would indicate a random model, whereas a perfect classification would have a point (0, 1). The area under the ROC curve (AUC) is 0.5 for the random and 1.0 for the perfect models, respectively. We calculated the 95% confidence intervals for each AUC. We used SPSS Version 16.0 (SPSS Inc., Chicago, IL, USA) for all analyses.

RESULTS

Our univariate analyses of 14 explanatory variables revealed five variables (A - area, E - elevation, I - isolation, S - stepping stone islands, and H - human visitation) that were significantly associated with the distribution of black rats on satellite islands in the Galápagos archipelago (Table 2). Two of these variables, area and elevation, were highly correlated ($r^2 = 0.822$). We omitted area from subsequent multivariate analyses because its significance was lower than that of elevation ($P = 0.228$ vs. $P = 0.040$, respectively). Univariate analyses of variables for house mice detected three variables (H, V - minimum EVI, and P - predator presence) that were important in explaining the distribution of mice in the archipelago (Table 2). Maximum likelihood estimates for alien bird and alien herp were not generated because alien birds were present on all satellite islands and alien herps were absent from all satellite islands.

Multivariate analysis of black rat presence/absence indicates two models adequately explained their distribution on islands (Table 3). However, the reduced model (I + S + H) had considerably more support than the full model ($w_i = 0.719$ vs. $w_i = 0.232$, respectively). In fact, examination of Akaike weights (w_i) of the individual variables suggests elevation is of minor importance, relative to the other variables, in explaining black rat distribution (Table 4). The large standard error of elevation relative to the parameter coefficient is also indicative of its minor contribution to the model (Table 5). Sums of Akaike weights (w_i; Table 4) indicate stepping stones and human visitation variables are of equal importance. However, on islands where black rats are present, the average distance from source island is greater on islands with stepping stones compared to those without ($\bar{X} =$ 528.5 m, SEM = 91.4 m vs. $\bar{X} =$ 192.6 m, SEM = 69.2, respectively). In contrast, for the islands where black rats are found, tourist visitation to islands did not appear to extend the distance they disperse from a source island compared to those with only occasional human visitation ($\bar{X} =$ 329.7 m, SEM = 85.4 m vs. $\bar{X} =$ 436.2 m, SEM = 96.6, respectively).

Results of model selection for house mice reveal all potential models had some support (Table 3). Although the human visitation model ranked highest, two other models (H

+ P and H + V were strongly competitive ($\Delta\text{AIC}_c = 1.194$ and $\Delta\text{AIC}_c = 1.567$, respectively). Among the three variables in the house mice models, Akaike weights (w_i; Table 4) and magnitude of standard errors (Table 5) indicate human visitation was most important in explaining their distribution in the Galápagos Islands.

Parameter estimates for black rats indicated that the probability of a rat occurring on an island decreased with increasing isolation (Table 5), whereas the probability of occurrence for a rat increased when a stepping stone island was present and the island was visited by tourists. In contrast, the coefficient for elevation suggests its influence on rat occurrence on islands was marginal. Therefore, we omitted it from the calculation of incidence functions (Fig. 2a). The incidence functions demonstrate the importance of stepping stone islands and tourist visitation on the distribution of black rats. On islands isolated from a source population by 1 km, with both stepping stones and tourist visitation, the probability of a rat occurring on an island is 98.1% compared to 39.8% on islands without either stepping stones or tourists (Fig. 2a). Model coefficients for house mice indicate the probability of their occurrence on an island increases when tourists and predators are present and when minimum EVI increases (Table 5). Incidence functions illustrate that both tourist visitation and the presence of predators influence the distribution of house mice on islands (Fig. 2b). However, tourist visits had a greater effect.

The best model for black rats explained > 50% of the variation in our dataset ($R^2_N = 0.528$; Table 3). Inclusion of elevation into the model did not improve the overall fit. The predictive power of the best model for black rats was high (AUC = 0.894, 95%CI = 0.823 - 0.965). Model discrimination did not improve with the full model (AUC = 0.894, 95%CI = 0.824 - 0.964). For house mice, the top three models fit similarly each explaining approximately 25% of the variation (Table 3). Of the three top models for house mice, the H + V model had the greatest predictive ability (AUC = 0.865, 95% CI = 0.743 – 0.987), whereas the two alternative models (H and H + P) had a lower predictive power and wide confidence intervals (AUC = 0.791, 95% CI = 0.538 – 1.043 and AUC = 0.791, 95% CI = 0.495 – 1.086, respectively).

DISCUSSION

Our results indicate that despite each species being influenced by anthropogenic factors, the distributions of black rats and house mice in the Galápagos Islands are structured by different processes. The occurrence of a black rat on an island appears to be driven primarily by factors related to immigration, whereas the incidence of house mice on an island is more complex.

As predicted from island biogoegraphic theory, the probability of a black rat occurring on a satellite island in the Galápagos Islands decreased the farther the island was from a source population of rats. In fact, isolation seems to be the principal driver of black rat incidence on Galápagos satellite islands, accounting for most of the variation in the best model (R^2_N = 0.327). In contrast, on offshore islands in the Mediterranean, distance from the mainland was found to have no effect on the incidence of mammals, including black rats (Sará & Morand, 2002). Furthermore, a meta-analysis to determine the factors influencing incidence of vertebrates on habitat islands found isolation was overall a poor predictor, especially so for mammals (Prugh *et al.*, 2008). Isolation was a significant factor explaining the distribution of black rats on New Zealand offshore islands, but island area surpassed it in importance (Russell & Clout, 2004). In our study, neither area or elevation emerged as a factor explaining the distribution of black rats.

On island systems where isolation was found to influence the incidence of species, it follows that stepping stones would also be a factor (Gilpin, 1980). However, the effect of a stepping stone is dependent on the dispersal abilities of the organism becoming greater as the organism's dispersal capacity decreases (MacArthur & Wilson, 1967; Gilpin, 1980). The presence of stepping stone islands in the Galápagos archipelago was related positively to the incidence of black rats on satellite islands approximately doubling the probability of a black rat occurring on an island ($\beta = 2.08$, I + S + H model) and contributing to an almost 3-fold increase in the dispersal distance of black rats. Surprisingly, the effect of a stepping stone on the probability of a black rat occurring on an island in the Galápagos archipelago is much less than the 100-fold increase predicted for an organism such as a rat with a rafting or swimming dispersal mode (MacArthur & Wilson, 1967). The observed effect of stepping stones in the Galápagos archipelago better fits that of pagile (passively dispersed) organisms, such as a wind-dispersed seeds, with a dispersal capacity greater than the range of isolation. The positive but relatively minimal influence of stepping stones on black rat incidence in the Galápagos archipelago suggests other factors are also playing a role in their dispersal.

Utilization of human transport by black rats would be expected to improve their vagility and extend their distribution within an archipelago. Anthropogenic factors were positively linked to the distribution of black rats on offshore islands in New Zealand (Russell & Clout, 2004). In our study, we found the presence of black rats on satellite islands was positively associated with increased human visitation to islands. Increased visitation could be responsible for minimizing the influence of stepping stones on the incidence of black rats on islands. However, it appears the effect of human visitation on black rat dispersal is relatively weak. Despite increasing the probability of black rats being present on an island, tourist visitation did not increase their mean dispersal distance in the Galápagos archipelago and when considered singly it accounted for relatively little of the overall variation in the best model ($R^2_N = 0.084$). An additional factor (which we did not evaluate) that may operate in conjunction with human transport to diminish the effect of stepping stone islands, is sea surface temperature (SST). In the Galápagos archipelago, mean SST is 23.5°C (range = 21.5°C – 25.7°C; Podestá & Glynn, 1997) and is the optimum level for survival for swimming rats (Bruner & Vargas, 1994). Thus, SST in the Galápagos archipelago could facilitate vagility in black rats and with human transport combines to lessen, but not negate, the influence of stepping stone islands on the incidence of black rats. Nevertheless, the combination of these three variables did not significantly reduce the importance of isolation as the principal factor determining the incidence of black rats on an island.

Understanding the mechanisms that determine the distribution of house mice on island systems harboring multiple species of alien rodents has proven difficult (Taylor, 1978; Russell & Clout, 2004). In the Galápagos archipelago, the distribution of house mice on satellite islands is sparse, but appears to be the result of a combination of biotic and abiotic factors (three of which were identified). We should emphasize that even the best model describing house mice distribution had a low coefficient of determination (Table 3).

Tourist visitation had the greatest influence on the incidence of house mice in the Galápagos Islands and explained almost a quarter of the variation in the best model (Table 3). Three of the four satellite islands invaded by house mice were visited by tourists and the fourth island is adjacent (< 140 m) to a major tourist site. Similarly, in New Zealand, all recorded invasions of offshore islands by house mice have been due to anthropogenic means (Taylor, 1975). Although house mice are known to cross open water distances up to 500 m (Burbidge, 2004), in general they appear to be poor over-water dispersers (Russell & Clout, 2005). This limitation is evident in the Galápagos archipelago. The four islands on which house mice were found are isolated from source populations by distances ranging from 302 m to 924 m yet mice failed to invade 21 islands nearer to source islands, several less than 50 m removed from a source population.

Two additional factors, primary productivity (minEVI) and predator presence, were found to influence the distribution of house mice though to a lesser extent than human visitation (Tables 3 & 4). The incidence of house mice on satellite islands was positively associated with primary productivity which has been linked to increased rodent abundance and diversity (Báez *et al.*, 2006; Reed *et al.*, 2006). However, our results differ somewhat from predictions based on island biogeographic theory (Lomolino, 2000). In an insular system with multiple species, interspecific differences in resource requirements would be expected to result in more energy intensive species (i.e. larger species) occupying islands that are larger or with higher primary productivity, whereas less energy intensive species should be found on smaller islands or those with lower productivity. In the Galápagos archipelago, this pattern was reversed with house mice being restricted to larger more productive islands, whereas black rats were able to establish on smaller islands with lower productivity (Fig. 3). The incidence of black rats on islands is independent of terrestrial primary productivity (or, its proxy, area) and may be due to their ability to use inputs from the marine system (Stapp & Polis, 2003a; 2003b). That house mice, an ecologically similar, but smaller species, appear to require islands with higher terrestrial primary productivity than black rats suggests other, potentially biotic factors, are involved in their distribution in the Galápagos archipelago.

We also found the incidence of house mice on satellite islands was positively linked with the presence of predators. A possible explanation for this association is that predator populations on an island prevent the establishment of black rats, in turn freeing house mice from interspecific competition or active predation. House mice and black rats are reported to compete for food and space (Yom-Tov *et al.*, 1999) and predation by Norway rats may exclude house mice from some islands (Moors, 1990). House mice in New Zealand demonstrated an increase in activity and a numerical increase following the removal of black rats (Innes *et al.*, 1995; Brown *et al.*, 1996). Similarly, house mice in the Galápagos archipelago exhibited competitive release when black rats were removed (Harris & Macdonald, 2007). However, we suspect the positive association of house mice with predator presence is random. It seems unlikely that predators would suppress the establishment of black rats but not house mice. Additionally, predator communities are similar across islands where black rats were present and absent as well as those where mice were found. A more likely explanation is that black rats have yet to arrive on these two islands.

Although the “alien rodent” term was not significant in the univariate analysis, we suspect black rats do limit the distribution of house mice on satellite islands. Our failure to detect an alien rodent interaction may be due to the sparse data for house mice. In addition to research (see above) demonstrating the competitive effects of black rats on house mice, results from this study support this hypothesis. Although correlative, the extinction of house mice from two islands (Seymour and Mosquera) following the invasion of black rats suggests rats negatively impacted mice. Further, house mice only occur on two satellite islands where black rats are absent.

Conclusions and recommendations

We used logistic regression analyses to determine the factors influencing the distribution of black rats and house mice in the Galápagos Islands. Our predictive model for black rats appears robust and indicates immigration processes are the principal mechanisms driving their intra-archipelago distribution and that factors associated with extinction have little to no effect on black rat incidence on an island. In short, if black rats reach an island there is high probability they will establish a viable population. Our model of house mice distribution was less robust resulting in predictions that are more tenuous. Thus, for house mice our findings are more speculative, if not intriguing. It appears the dispersal of house mice in the archipelago is strongly influenced by anthropogenic movement, however, their likelihood of establishing a population on an island is dependent on the absence of black rats.

Undoubtedly, there are variables we did not identify that would improve the fit of the black rat and house mouse models. Further refinement of some the variables we examined would provide insight into the dynamics of rodent dispersal, such as changing human visitation from a binary to a continuous variable. Additional sampling of islands would improve the analyses and strengthen the model predictions, especially those for house mice.

Nevertheless, our results have important implications for the management of alien rodents in the Galápagos Islands. Although, the feasibility of eradicating rodents from islands has improved greatly, the effort and costs remain high (Howald *et al.*, 2007). Therefore, it is incumbent upon managers in the Galápagos archipelago to incorporate the risk of reinvasion in the planning for rodent eradications (Clout & Russell, 2008). Specifically, islands proposed for eradication of blacks rats should be evaluated in the context of our model. Distance from a source population of black rats is paramount, as is the presence of stepping stone islands and the level of human visitation. The potential for house mice to invade an island freed of rats should be considered as well.

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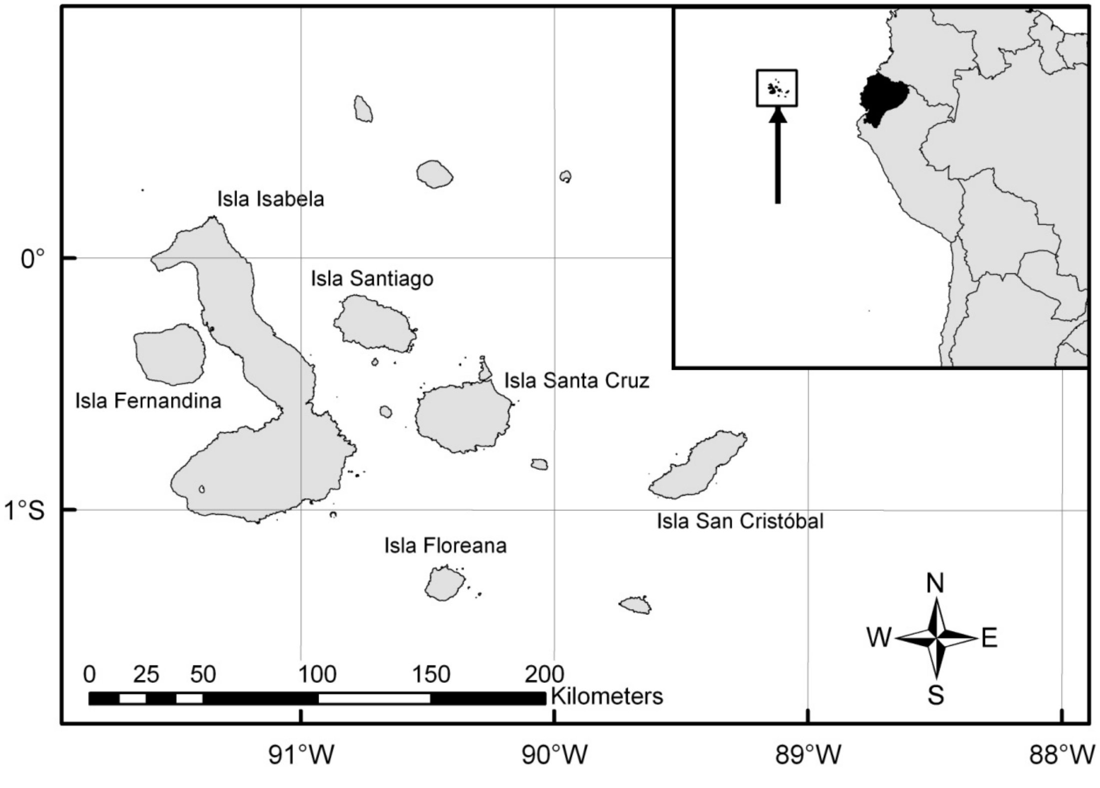

Figure 1 The Galápagos archipelago of Ecuador and its location relative to South America.

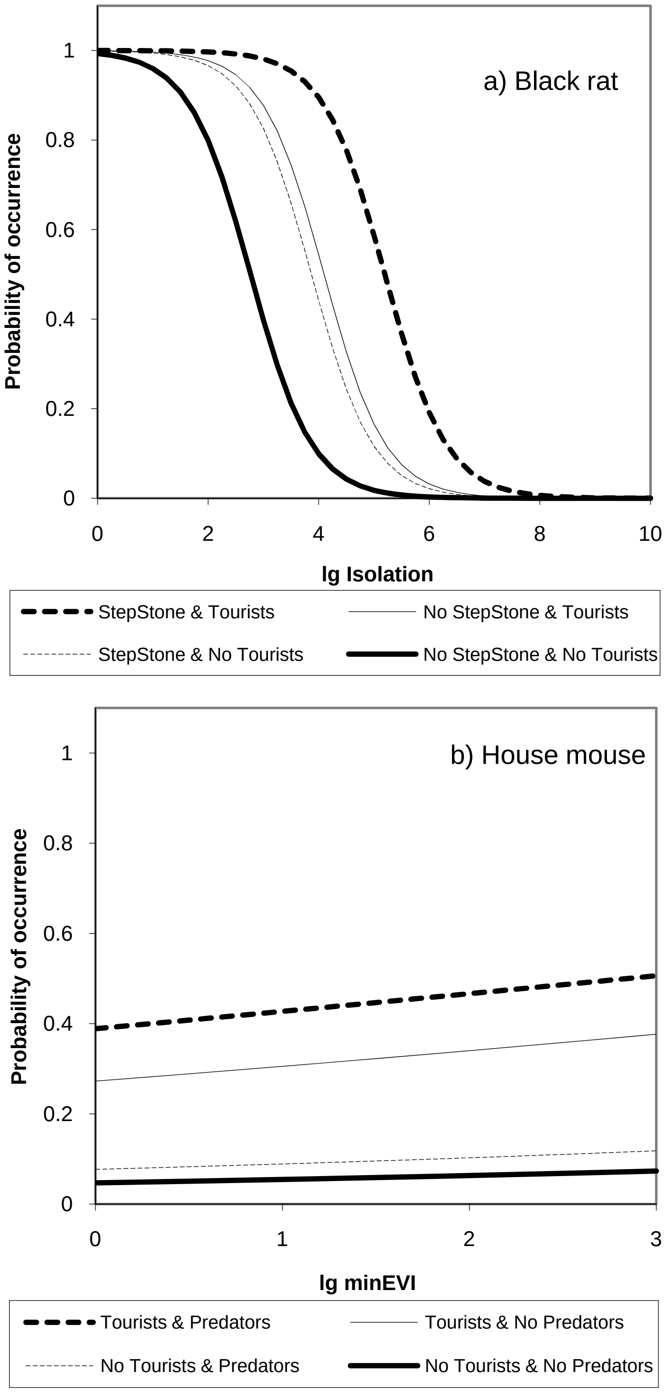

Figure 2 Incidence functions showing the effect of environmental and anthropogenic variables on the probability of occurrence of black rats and house mice on satellite islands in the Galápagos archipelago. Coefficients were derived from model-averaged parameter estimates.

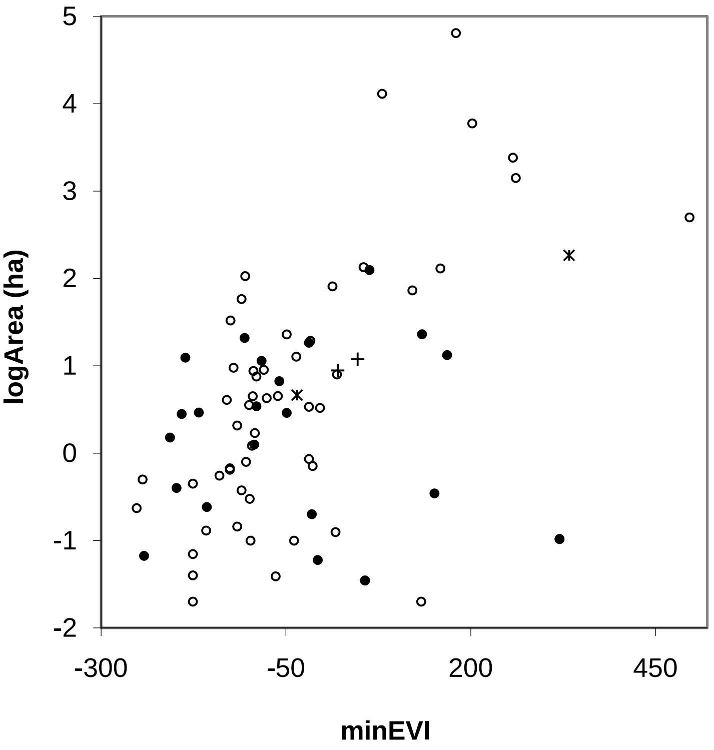

Figure 3 Distribution function of black rats and house mice on satellite islands in relationship to island area and primary productivity (minEVI) in the Galápagos archipelago. Symbols are: islands with no rodents present (◦); black rats present (•); house mice present (+), and black rats and house mice present (∗). Analyses were conducted using log-transformed (base 10) minEVI values; raw values are presented here for visual clarity.

Table 1 Explanatory variables examined in the analyses. Variables values apply to each of the 81satellite islands, except where specified.

Variable	Description	Data range
Continuous		
Area*	Land area (ha).	0.02 – 64,248
Elevation*	Maximum elevation (m).	1 – 1,570
Isolation*	Distant to nearest island (m).	8 – 181,083
MeanEVI*	Index for mean primary productivity.	65 – 1,798
MaxEVI*	Index for maximum primary productivity.	340 – 5,729
MinEVI*	Index for minimum primary productivity.	335 – 676
Human population†	Human population size of source island	0 – 10,000
Binary/Categorical		
Human visitation	Tourist site/occasional visitation	0 / 1
Stepping stone	Presence/absence of stepping stone island between island and mainland.	0 / 1
Alien bird	Presence/absence of alien birds established.	0 / 1
Alien herp	Presence/absence of alien lizards established.	0 / 1
Predator	Presence/absence of mammalian or bird predators of rodents.	0 / 1
Rodent	Presence/absence of other alien or native rodents.	0 / 1
Alien rodent	Presence/absence of other alien rodents.	0 / 1

* log- transformed (base 10).

† Human population values used in analyses are from the period when sampling occurred and differ from current population levels.

Table 2 Results from univariate analyses of explanatory variables in alien rodent distribution models. *P*-values were derived from the log-likelihood ratio test in logistic regression analysis. Significance of $P < 0.25$ was used as a cutoff for inclusion in multivariate model building (Mickey & Greenland, 1989). Maximum likelihood estimates were not generated for alien bird or alien herp (see Text).

Variable	Black rat	House mouse
	P	*P*
Continuous		
Area*	0.228†	0.336
Elevation*	0.040	0.929
Isolation*	0.000	0.372
MeanEVI*	0.634	0.420
MaxEVI*	0.482	0.847
MinEVI*	0.974	0.114
Human population	0.787	0.460
Binary/Categorical		
Human visitation	0.026	0.024
Stepping stone	0.010	0.442
Alien bird	na	na
Alien herp	na	na
Predator	0.613	0.121
Rodent	0.835	0.549
Alien rodent	0.697	0.477

* Variables log transformed (base 10).

† Area was not included in multivariate analyses because of its high correlation with Elevation (see Methods).

Table 3 Model selection results from logistic regression analyses on the occurrence of two alien rodents on satellite islands in the Galápagos archipelago. Models are the "confidence set" and ranked by ΔAIC_c. *K* = the number of parameters in a model, including the intercept; ΔAIC_c = the difference between the AIC_c of the best model and AIC_c of a given model; w_i = the Akaike weight; R^2_N = the coefficient of determination (Nagelkerke, 1991).

Species	Model*	*K*	ΔAIC_c	w_i	R^2_N
Black rat	I + S + H	4	0.000	0.719	0.528
	E + I + S + H	5	2.261	0.232	0.528
House mouse	H	2	0.000	0.367	0.223
	H + P	3	1.194	0.202	0.256
	H + V	3	1.567	0.168	0.243
	H + V + P	4	3.091	0.078	0.267
	P	2	3.214	0.074	0.107
	V	2	3.592	0.061	0.093
	V + P	3	4.009	0.050	0.157

* Model variables are: I = isolation, S = stepping stone, H = human visitation, E = elevation, P = predator, V = minEVI (see text and Table 1 for detailed explanation of variables).

Table 4 Relative importance of the explanatory variables among the candidate models for each species. Values are the sum of Akaike weights (w_i) within the "confidence set" of models containing the given variable.

	Model Variables*					
Species	E	I	S	H	P	V
Black rat	0.232	0.951	0.951	0.951		
House mouse				0.816	0.404	0.357

* Model variables are: E = elevation, I = isolation, S = stepping stone, H = human visitation, P = predator, V = minEVI (see text and Table 1 for detailed explanation of variables).

Table 5 Model-averaged parameter estimates (*β*) and 95% confidence intervals in parentheses for the effect of explanatory variables on the incidence of black rats and house mice on 81 islands in the Galápagos archipelago.

	Black rat				House mouse		
	β	SE	(95% CI)		*β*	SE	(95% CI)
Intercept	4.97	1.43	(2.11, 7.82)	Intercept	-3.02	0.72	(-4.45, -1.58)
Elevation	-0.02	0.15	(-0.31, 0.28)	Human visitation	2.04	1.08	(-0.12, 4.19)
Isolation	-1.79	0.51	(-2.82, -0.77)	Predator presence	0.53	0.60	(-0.67, 1.72)
Stepping stone	1.97	0.72	(0.55, 3.40)	minEVI	0.16	0.21	(-0.26, 0.57)
Human visitation	2.38	0.89	(0.60, 4.16)				