

Chapter 2

Colonization of Galápagos Birds: Identifying the Closest Relative and Estimating Colonization

Eloisa H.R. Sari and Jennifer L. Bollmer

Abstract Native Galapagos bird species show varying colonization histories, with lineages representing a wide age distribution and various geographic origins. Of the taxa studied, founding lineages arrived from less than 300,000 years ago (e.g., Band-rumped Storm Petrel, hawk) up to 2.0–5.5 million years ago (e.g., dove, finches, mockingbirds). Some of these earlier lineages reached Galapagos before the youngest of the current islands formed, so they must have first colonized what are now the eastern islands. While the exact origin of colonizing lineages cannot always be determined, all the native land birds studied originated from the New World, where their closest living sister taxa breed. The closest related lineages to Galapagos seabirds are generally found elsewhere in the Pacific Ocean. Galapagos species vary in their diversification patterns post-colonization, with factors such as life history traits, island geology, and trade winds affecting the genetic patterns described. The mockingbirds and Darwin's finches radiated into multiple species, while most others have not, probably due to high rates of gene flow (e.g., dove) or lack of time since colonization (e.g., hawks, warblers). Humans were responsible for the introduction of 12 bird species to Galapagos, as well as the introduction of invasive invertebrates, parasites, and pathogens, which pose a serious threat to native Galapagos fauna. Continued research into colonization histories and evolutionary units of native lineages will aid our understanding of host-parasite interactions and better inform conservation management decisions.

Keywords Biogeography • Endemic birds • Island colonization • Phylogeny • Species ages

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2.1 Introduction: Factors Influencing Galapagos Colonization

The corollary of the famous *Theory of Island Biogeography* proposed by MacArthur and Wilson (1967) says that the number of species occupying a given island is a function of the colonization rate and the extinction rate. The colonization rate depends on the distance of the island from the colonizing source (continent or other larger islands), while the extinction rate depends on the carrying capacity of the island, normally a function of island area. Therefore, islands that are more isolated have lower colonization rates, and smaller islands have higher extinction rates. Species colonization implies not just arrival or immigration, but also establishment on the island. In this chapter, we are concerned with the colonization history of bird species that successfully established on the Galapagos Islands. Therefore, we are interested in describing the patterns of arrival for bird species, such as their arrival time and the geographic origin of their colonizing source, as well as the evolutionary history of these species on the islands, such as their population structure or lineage diversification. First, we summarize information necessary for our understanding of colonization history of Galapagos birds—the geography and geology of the archipelago and ocean currents and wind patterns that could affect colonization.

2.1.1 Geography and Geology

The Galapagos archipelago is oceanic, formed by volcanic activity, and was never connected to other landmasses. It sits on the Nazca Plate about 1000 km from South America (off Ecuador) and 1300 km from Costa Rica in Central America. Its isolation probably explains the small number of terrestrial lineages that have colonized the islands (Parent et al. 2008). There are 13 islands larger than 10 km² and many other smaller ones. The ages of the islands increase from west to east; a volcanic hotspot gives rise to the islands, which then drift eastward with the movement of the Nazca plate. The current islands range in age from about 5 million years for the oldest ones of San Cristóbal and Española, at the southeastern edge of the archipelago, to less than 300,000 years for the youngest and most western island of Fernandina (Fig. 2.1; Geist 1996). However, older, now submerged seamounts occur at the Carnegie Ridge, southeast of the archipelago, so colonization times of Galapagos biota could extend to at least 9 million years ago (White et al. 1993). Knowing the age of the archipelago and each one of its islands is important in order to better understand how species colonized the islands—which islands were available to be colonized, where the differentiation of each species started, and how they diversified across the islands.



Fig. 2.1 Ages of central Galapagos Islands proposed by Geist (1996). Ages are given in million years (my) below island names. Map of the Galapagos Archipelago with main islands was modified from NordNordWest (<https://commons.wikimedia.org/wiki/User:NordNordWest>) under the terms of the GNU Free Documentation License

2.1.2 Ocean Currents and Trade Winds

Ocean and wind currents may facilitate species' arrival to Galapagos, bringing new colonizers. The prevailing ocean current in Galapagos is the Humboldt (or Peru) Current. It flows northward from the Antarctic region along the west coast of South America, and, as it passes northern Peru and Ecuador, it is deflected westward, joining the South Equatorial Current and they both run toward Galapagos (Fig. 2.2). The Humboldt Current brings very cold waters from the south and is responsible for the dry and moderate climate of Galapagos and its cool waters from June to November. Colonizers from South America such as penguins and fur seals could

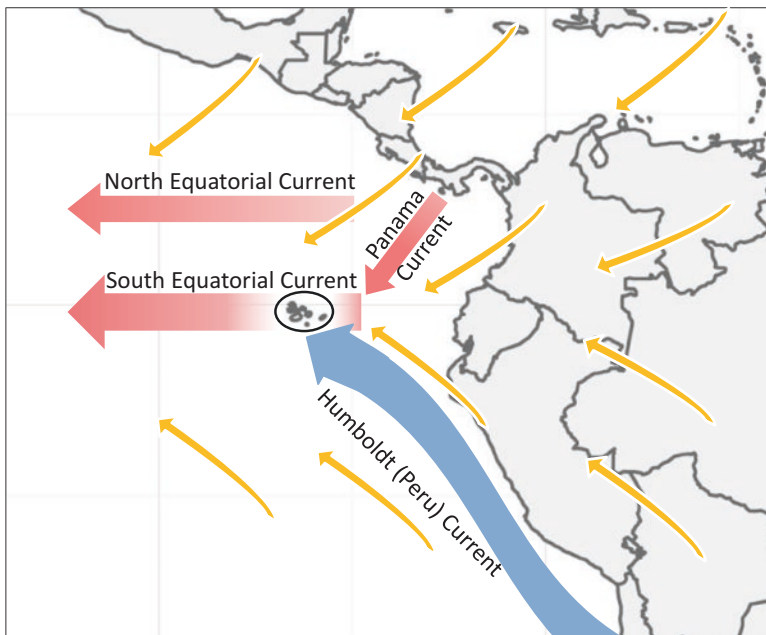


Fig. 2.2 Humboldt, Equatorial, and Panama ocean currents are responsible for the climate in Galapagos. Trade winds (represented by *yellow thin arrows*) blow southeasterly in the Southern hemisphere and northeasterly in Northern hemisphere. Galapagos Archipelago is within the *circle*

have followed this ocean current (Baker et al. 2006; Yonezawa et al. 2009), or simply intersected it and reached Galapagos via passive drifting, such as the leaf-toed geckos (*Phyllodactylus* spp., Torres-Carvajal et al. 2014). Around November, due to atmospheric changes in the region, the South Equatorial and the Humboldt currents flow slower, and the Panama Current flowing from Central America prevails in Galapagos. Warmer waters replace the Antarctic waters, and the archipelago experiences higher temperatures from January to May. While this ocean current has rarely been associated with colonization of Galapagos, trade winds have likely facilitated the arrival of colonizers from Central America and the Caribbean, such as Darwin's finches and the Galapagos mockingbirds. In the tropics, prevailing trade winds blow from the northeast and southeast toward the Equator (Fig. 2.2). These winds also are important at smaller scales, such as within the Galapagos archipelago. Several studies have considered the trade winds to explain patterns of colonization and gene flow from southeastern islands to northwestern islands in Galapagos (e.g., diversification of Galapagos mockingbirds (Arbogast et al. 2006) and gene flow in Nazca boobies (Levin and Parker 2012)).

2.1.3 *Estimating Time for Colonization Events*

According to Kimura's neutral theory of molecular evolution, the majority of nucleotide substitutions detected in a gene are "nearly neutral," i.e., are not under selection, and most of the variation between species accumulates randomly because of genetic drift (Kimura 1968). As a result, homologous DNA sequences evolve at virtually the same rate in different species and populations. According to this logic, therefore, two species accumulate nucleotide substitutions at the same rate in a given DNA region, and the genetic distance between these two species will be proportional to their divergence time. This rate of evolution is referred to as a molecular clock. The use of a molecular clock allows the estimation of the time when two sister lineages originated, or started diverging from each other after a phylogenetic splitting event. This event may represent, for example, the colonization of an island followed by the isolation of the island lineage in relation to its colonizing ancestors.

The molecular clock can "tick" faster or slower depending on the DNA region and the coded protein, but it is more or less constant for different but related lineages, assuming they are under similar selective pressures. The speed of the ticking is the nucleotide substitution rate (or molecular evolution rate, mutation rate, rate of sequence divergence), and this rate has been estimated for several DNA regions and taxonomic groups. Weir and Schluter (2008) estimated the nucleotide substitution rate for the mitochondrial cytochrome b gene to be 2.07% per million years for several passerine birds (Passeriformes). This means that, if the genetic distance between two bird species is 2.07% when using cytochrome b sequences, these two bird lineages diverged, or became independent, 1 million years ago (MYA). Conversely, Quinn (1992) estimated a rate ten times larger (21% per million years) for domain I of the mitochondrial control region, a non-coding region, in the Snow Goose.

Besides using a direct measure of genetic divergence between lineages to calculate their divergence time, a phylogenetic approach can also give this information. The application of molecular clock methods when estimating phylogenies allows for a relaxation of the clock, to include uncertainties and clock calibration points. Uncertainties can be incorporated by allowing substitution rates to vary with time and between lineages in the phylogeny. Calibration points can be used to restrain the phylogeny by adding the maximum or minimum age of a fossil or a biogeographical event on the tree. Several software packages are available to estimate divergence times using a phylogeny, calculated by means of maximum likelihood or Bayesian inference (see Rutschmann 2006 for a review of methods). An in-depth review of molecular dating is not the goal of this chapter, but a variety of methods were used to estimate colonization times of Galapagos taxa, and we need to take that into consideration when comparing the colonization histories of different species.

2.2 Colonization History of Native Species

Native species are those that naturally colonized and occur in a location, and were not introduced by humans. Some species considered native to one region may also be migrants and reproduce elsewhere. Over 2000 species of terrestrial invertebrates, about 530 species of fishes, and 119 species of other vertebrates (mammals, birds, and reptiles) have been recorded as non-migrant natives in the Galapagos archipelago (Bungartz et al. 2009). Fifty-seven of these taxa are marine and terrestrial birds. Of those taxa, 45 are considered endemics (Jiménez-Uzcátegui et al. 2015), which means they differentiated from their ancestral lineages sufficiently to be considered separate species, and this includes most of the terrestrial birds. Twelve taxa are considered indigenous (Jiménez-Uzcátegui et al. 2015), meaning that they have breeding populations in Galapagos but also somewhere else in the world. The indigenous taxa of Galapagos are composed primarily of seabirds and shorebirds, as well as a single terrestrial species, the Dark-billed Cuckoo (*Coccyzus melacoryphus*), which has breeding populations in forests of South America, and probably represents the most recent natural arrival for land birds (Jackson 1993).

The colonization histories of about half of the native taxa (29) have been systematically studied, revealing their geographic origins, closest extant relatives, and time since arrival to the islands (Fig. 2.3; Table 2.1). The large proportion of studied taxa may imply that the history of bird colonizations in Galapagos is well understood. However, these 29 taxa evolved from only 13 founding lineages; in fact, just two lineages gave rise to 14 species of Darwin's finches and four species of Galapagos mockingbirds. Therefore, 28 out of the 41 actual bird colonization events, or 68% of these events, have not yet been studied (Table 2.2). This suggests that we still have only a limited understanding of how and when native species arrived in the archipelago. Specifically, this lack of knowledge is a result of limited available data regarding the continental distributions and phylogenetic positions of the potential sister taxa of Galapagos birds (Parent et al. 2008).

The colonization of the Galapagos archipelago by birds occurred over a wide range of time-periods. The oldest estimated arrival times are for the Galapagos mockingbirds (1.6–5.5 MYA; Arbogast et al. 2006) and the Darwin's finches (2.3 MYA; Sato et al. 2001), while the indigenous population of Band-rumped Storm Petrels (*Oceanodroma castro*) is estimated to be the most recent arrival (fewer than 200,000 years ago; Smith et al. 2007). The Magnificent Frigatebird (*Fregata magnificens magnificens*) and the Yellow Warbler (*Setophaga petechia aureola*) are considered the youngest endemic avian subspecies in Galapagos, but the Galapagos Hawk (*Buteo galapagoensis*) is the youngest taxon with full species status; all three of these taxa were estimated to have arrived around 300,000 years ago (Bollmer et al. 2006; Chaves et al. 2008; Amaral et al. 2009; Hailer et al. 2011). Other birds, such as flycatchers, doves, penguins, cormorants, and petrels, colonized the archipelago in intermediate time-periods (Fig. 2.3).

Estimates of arrival times suggest that the ancestors of the Darwin's finches, the Galapagos mockingbirds, and the Galapagos Dove must have initially colonized the

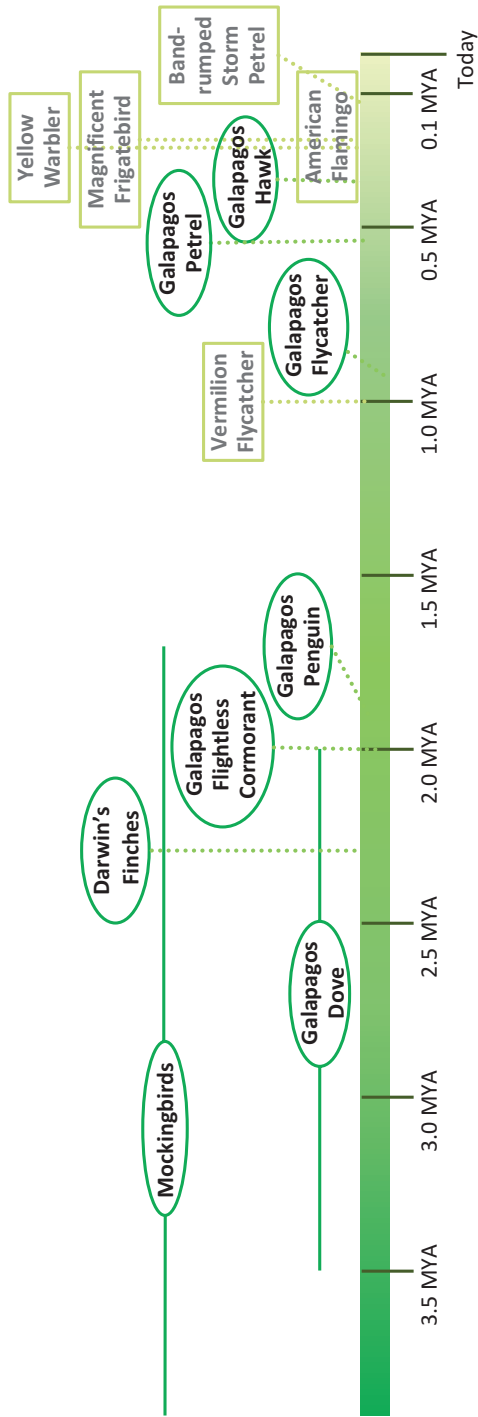


Fig. 2.3 Colonization timeline for Galápagos native birds. Maximum and minimum estimates for colonization are indicated by *horizontal bars*. MYA is million years ago. Endemic species are inside *green circles*, non-endemic species are in *yellow rectangles*. Colonization times were extracted from publications cited as in Table 2.1

Table 2.1 Colonization information available for Galapagos native bird species

English name	Time since colonization	Putative geographic origin	Closest living relatives	Genetic structure in Galapagos	References
<i>Oceanodroma castro</i> Band-rumped Storm Petrel	154,000–192,000	Pacific	Conspecific Pacific populations	Sympatric seasonal populations are genetically differentiated	Smith and Friesen (2007) and Smith et al. (2007)
<i>Fregata magnificens magnificens</i> Galapagos Magnificent Frigatebird	247,000	Unknown	Unknown	Not tested	Hailer et al. (2011)
<i>Setophaga petechia aureola</i> Yellow Warbler	268,000	Central America	<i>Setophaga petechia erithachorides</i> /S. p.xanthotera	Some islands are genetically differentiated	Chaves et al. (2012)
<i>Buteo galapagoensis</i> Galapagos Hawk	126,000–340,000	North America	<i>Buteo swainsoni</i> (Swainson's Hawk)	All islands are differentiated	Bollmer et al. (2005, 2006), Amaral et al. (2009) and Koop et al. (2014)
<i>Phoenicopterus ruber</i> American Flamingo	70,000–350,000	Caribbean/South America	Conspecific Caribbean populations	Not tested	Frias-Soler et al. (2014)
<i>Pterodroma phaeopygia</i> Galapagos Petrel	550,000	Tropical Pacific	<i>Pterodroma sandwicensis</i> (Hawaiian Petrel)	Some islands are genetically differentiated	Friesen et al. (2006) and Welch et al. (2011)
<i>Myiarchus magnirostris</i> Galapagos Flycatcher	850,000	Central America	<i>Myiarchus tyrannulus</i> (Brown-crested Flycatcher)	Some islands are genetically differentiated	Sari and Parker (2012)
<i>Pyrocephalus rubinus</i> Vermilion Flycatcher	1,000,000	South America	All other <i>Pyrocephalus rubinus</i> subspecies	Three lineages: <i>P.r. dubius</i> , and 2 lineages within <i>P.r. nanus</i>	Carmi et al. (2016)
<i>Spheniscus mendiculus</i> Galapagos Penguin	1,900,000	Peru	<i>Spheniscus humboldti</i> (Peruvian Penguin)	Panmixia	Nims et al. (2008) and Subramanian et al. (2013)

English name	Time since colonization	Putative geographic origin	Closest living relatives	Genetic structure in Galapagos	References
<i>Phalacrocorax harrisi</i> Galápagos Flightless Cormorant	2,000,000	Americas	<i>Phalacrocorax auritus</i> (Double-crested Cormorant)/ <i>P. brasilianus</i> (Neotropic Cormorant)	All populations and islands are differentiated	Duffie et al. (2009) and Kennedy et al. (2009)
<i>Zenaida galapagoensis</i> Galapagos Dove	2,000,000–3,510,000	Unknown	<i>Zenaida auriculata</i> (Eared Dove) and <i>Z. graysoni</i> (Socorro Dove)/ <i>Z. macroura</i> (Mourning Dove)	Panmixia	Johnson and Clayton (2000), Santiago-Alarcon et al. (2006) and Valente et al. (2015)
<i>Certhidea</i> spp., <i>Cactospiza</i> spp., <i>Geospiza</i> spp., <i>Camarhynchus</i> spp., <i>Platyspiza crassirostris</i> Darwin finches (14 species)	2,300,000	Caribbean	<i>Tiaris fuliginosus</i> (Sooty Grassquit)/ <i>T. obscurus</i> (Dull-colored Grassquit)	Panmixia for <i>Camarhynchus</i> spp. and <i>Geospiza fuliginosa</i> . Some islands are genetically differentiated for other species	Sato et al. (2001), Burns et al. (2002), Petren et al. (2005), Burns et al. (2014) and Farrington et al. (2014)
<i>Mimus</i> spp. Galapagos mockingbirds (4 species)	1,600,000–5,500,000	Caribbean	<i>Mimus gundlachii</i> (Bahama Mockingbird)	All islands are differentiated for <i>Mimus parvulus</i>	Arbogast et al. (2006), Hoeck et al. (2010) and Lovette et al. (2012)
<i>Information from studies not focusing on colonization of Galapagos taxa</i>					
<i>Sula granti</i> Nazca Booby	<1,100,000	Unknown	<i>Sula dactylatra</i> (Masked Booby)	Some islands are genetically differentiated	Friesen et al. (2002), Patterson et al. (2011) and Levin and Parker (2012)
<i>Sula nebowxii excisa</i> Blue-footed Booby	Unknown	Peru and Ecuador	Conspecific populations from Peru and Ecuador	Panmixia	Taylor et al. (2011)

(continued)

Table 2.1 (continued)

English name	Time since colonization	Putative geographic origin	Closest living relatives	Genetic structure in Galapagos	References
<i>Sula sula websteri</i> Red-footed Booby	Unknown	Unknown	Conspecific Pacific populations	Not tested	Steeves et al. (2003) and Morris-Pocock et al. (2010)
<i>Oceanodroma tethys</i> Lava Gull	Unknown	Mexico	<i>Halocryptena microsoma</i> (Least Storm Petrel)	Not tested	Nunn and Stanley (1998) and Kennedy and Page (2002)
<i>Puffinus subalaris</i> Galapagos Shearwater	Unknown	Central Pacific	<i>Puffinus nativitatis</i> (Christmas Shearwater)	Not tested	Austin et al. (2004)
<i>Leucophaeus fuliginosus</i> Lava Gull	Unknown	North/Central America	<i>Leucophaeus pipixcan</i> (Franklin's Gull)	Not tested	Pons et al. (2005)
<i>Creagrurus furcatus</i> Swallow-tailed Gull	Unknown	Unknown	Basal to all other gull species (Laridae)	Not tested	Pons et al. (2005)
<i>Anous stolidus</i> Brown Noddy	<1,000,000	Unknown	Unknown	Not tested	Cibois et al. (2016)
<i>Phoebastria irrorata</i> Waved Albatross	Unknown	Unknown	Basal to all other <i>Phoebastria</i> spp.	Not tested	Kennedy and Page (2002)

Table 2.2 Galapagos native bird species for which colonization is unknown

Species name	English Name	Order	Family	Status	IUCN Status
<i>Oceanites gracilis galapagoensis</i>	Elliot's Storm Petrel	Procellariiformes	Hydrobatidae	Endemic	NE
<i>Phaethon aethereus</i>	Red-billed Tropicbird	Phaethontiformes	Phaethontidae	Indigenous	LC
<i>Ardea alba</i>	Great Egret	Pelecaniformes	Ardeidae	Indigenous	LC
<i>Ardea herodias cognata</i>	Great Blue Heron	Pelecaniformes	Ardeidae	Endemic	NE
<i>Butorides striata sundevalli</i>	Striated Heron	Pelecaniformes	Ardeidae	Endemic	NE
<i>Nyctanassa violacea pauper</i>	Yellow-crowned Night Heron	Pelecaniformes	Ardeidae	Endemic	NE
<i>Pelecanus occidentalis urinator</i>	Brown Pelican	Pelecaniformes	Pelecanidae	Endemic	NE
<i>Fregata minor</i>	Great Frigatebird	Suliformes	Fregatidae	Indigenous	LC
<i>Anas bahamensis galapagensis</i>	White-cheeked Pintail	Anseriformes	Anatidae	Endemic	NE
<i>Gallinula galeata</i>	Common Gallinule	Gruiformes	Rallidae	Indigenous	LC
<i>Laterallus spilonota</i>	Galapagos Rail	Gruiformes	Rallidae	Endemic	VU
<i>Neocrex erythrops</i>	Paint-billed Crake	Gruiformes	Rallidae	Indigenous	LC
<i>Haematopus palliatus galapagensis</i>	American Oystercatcher	Charadriiformes	Haematopodidae	Endemic	NE
<i>Himantopus mexicanus</i>	Black-necked Stilt	Charadriiformes	Recurvirostridae	Indigenous	LC
<i>Onychoprion fuscatus crissalis</i>	Sooty Tern	Charadriiformes	Sternidae	Indigenous	LC
<i>Coccyzus melacoryphus</i>	Dark-billed Cuckoo	Cuculiformes	Cuculidae	Indigenous	LC
<i>Asio flammeus galapagoensis</i>	Short-eared Owl	Strigiformes	Strigidae	Endemic	NE
<i>Tyto alba punctatissima</i>	Barn Owl	Strigiformes	Tytonidae	Endemic	NE
<i>Progne modesta</i>	Galapagos Martin	Passeriformes	Hirundinidae	Endemic	EN

Classification of indigenous or endemic and IUCN red-list assessments are according to Jiménez-Uzcátegui et al. (2015). IUCN status are EN endangered, LC least concern, VU vulnerable, NE Not Evaluated

islands of San Cristóbal, Española, and Santa Fe, because those were the first islands to appear about 2–6 MYA (Geist 1996); none of the other islands existing today were exposed when the ancestors of those birds arrived. The geography of the archipelago changed over time, and by about 1 million years ago, all of the currently existing islands, with the exception of Isabela and Fernandina, had emerged. Therefore, ancestors of the flycatchers, warblers, penguins, cormorants, and hawks had a larger number of suitable islands available for colonization. Of the non-avian species in Galapagos, the ancestors of the Galapagos leaf-toed geckos (*Phyllodactylus* spp.), the Galapagos iguanas (*Amblyrhynchus cristatus* and *Conolophus* spp.), the *Galapaganus* weevils, and the Band-winged Grasshopper (*Sphingonotus fuscoirroratus*) all likely colonized Galapagos more than seven MYA, before the presently existing islands were exposed (Sequeira et al. 2000; Torres-Carvajal et al. 2014; Husemann et al. 2015; MacLeod et al. 2015). These species arrived on islands that are currently underwater seamounts southeast of the archipelago (White et al. 1993; Geist 1996). Therefore, earlier colonizing lineages had the opportunity to colonize the islands progressively, from older to younger islands (but see Sequeira et al. 2008), or from southeast to northwest, while the pattern of interisland colonization is not so clear for more recent colonists.

Various geographical origins have been proposed for the lineages that colonized Galapagos. Most of the studied endemic Galapagos vertebrates originated in South America, including the rice rats (*Oryzomys* spp., *Nesoryzomys* spp., *Megaoryzomys* spp.) and all of the lineages of reptiles: leaf-toed geckos, lava lizards (*Microlophus* spp.), tortoises (*Geochelone nigra*), and iguanas (Parent et al. 2008). In contrast, the sister species of the Galapagos Sea Lion (*Zalophus wolfebaeki*) is the California Sea Lion (*Z. californianus*) from North America (Wolf et al. 2007). Despite the fact that insects represent the majority of the Galapagos faunal diversity (1500 species), the geographic origins of only a few insect lineages have been identified. The majority of studied insects colonized Galapagos from South America as well, including several beetle genera (Parent et al. 2008) and the *Galapaganus* weevils (Sequeira et al. 2000). The species most related to the Galapagos moths (*Galagete* spp.) and the Band-winged Grasshopper, however, are only found in the Caribbean. While colonization from the Caribbean is possible, it may be that the South American ancestors of these species have gone extinct (in the case of the grasshopper; Husemann et al. 2015) or simply were never documented on the continent (in the case of the moths; Schmitz et al. 2007).

The colonizing sources of the Galapagos terrestrial birds studied to date can all be linked to a region in the New World (Fig. 2.4). Darwin's finches and the Galapagos mockingbirds resulted from lineage diversifications that originated in the Caribbean or Central America (Sato et al. 2001; Burns et al. 2002, 2014; Arbogast et al. 2006), while the sister lineages of the Galapagos Flycatcher (*Myiarchus magnirostris*) and the Yellow Warbler (*Setophaga petechia aureola*) are distributed only in Central America (Chaves et al. 2012; Sari and Parker 2012). Galapagos Hawks (*Buteo galapagoensis*) are most closely related to Swainson's Hawks (*B. swainsoni*), which breed in North America (Bollmer et al. 2006; Amaral et al. 2009), and the ancestors of Vermilion Flycatchers (*Pyrocephalus rubinus*) may have originated from South America (Carmi et al. 2016), but both belong to lineages that are typically migratory.

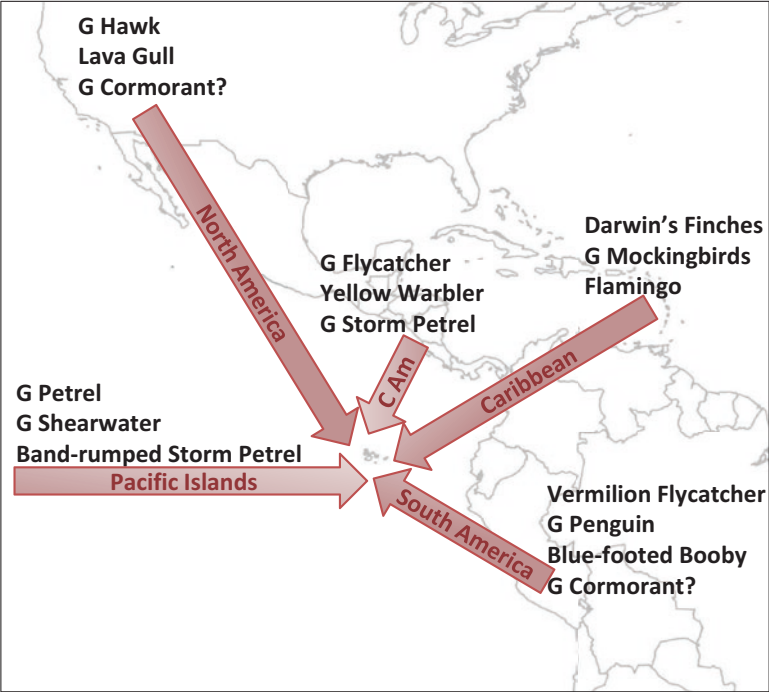


Fig. 2.4 Colonization origins of Galapagos native birds. G is Galapagos; C Am is Central America; question mark after Cormorant refers to different possible origins for this species. Species names are in Table 2.1

Conversely, the closest relatives of Galapagos seabirds occur in other locations in the Pacific Ocean, including isolated archipelagos. The Galapagos Petrel (*Pterodroma phaeopygia*) is sister to the Hawaiian Petrel (*P. sandwichensis*; Welch et al. 2011), and the Galapagos Shearwater (*Puffinus subalaris*) is sister to the Christmas Shearwater (*Puffinus nativitatis*) from Central Pacific islands (Austin et al. 2004).

In this chapter, we will review and present all of the colonization histories that are available in the literature for native Galapagos bird species in a comparative fashion. We present these histories in detail below, and we include information regarding lineage diversification and population genetic structure of the lineages—if any—after becoming established in Galapagos.

2.2.1 Terrestrial Birds Show Different Patterns of Colonization

Among the 28 terrestrial birds found in Galapagos, two colonization events resulted in the majority of species: the Darwin's finches (14 species) and the mockingbirds (four species). These two groups of species, as well as the Galapagos Dove, represent the oldest terrestrial bird lineages in the archipelago, with colonization times older than 2 million years. The doves, however, have not diversified on the islands.

Galapagos Dove The Galapagos Doves (*Zenaida galapagoensis*) have high levels of gene flow and no evidence of genetic structure among five islands—Santa Fe, Santiago, Genovesa, Española, and Santa Cruz—revealing they can readily disperse over water throughout the archipelago (Santiago-Alarcon et al. 2006). Taxonomic work had previously proposed two subspecies in Galapagos: *exsul* on the northern islands of Darwin and Wolf, and *galapagoensis* on the other islands. Indeed, doves from Wolf Island seem to differ in sexual size dimorphism compared to doves from southern islands (Santiago-Alarcon and Parker 2007). Samples from Darwin and Wolf, however, need to be included in population genetic studies so we can better understand the evolution of the Galapagos Doves in the archipelago.

Johnson and Clayton (2000) proposed a phylogeny for the genus *Zenaida* using mitochondrial and nuclear DNA sequences. This phylogeny revealed that the Galapagos Dove is sister to a clade that later split into Mourning (*Z. macroura*) and Eared (*Z. auriculata*) Doves. Mourning Doves occur in North America and Eared Doves are found in South America; therefore, ancestors of Galapagos Doves originated in the New World, but a more precise geographic origin is difficult to pinpoint. Johnson and Clayton (2000) used a previously published substitution rate to compare the genetic divergences between *Zenaida* species and they estimated the colonization time for the Galapagos Dove to be just over two MYA. However, Valente et al. (2015) rebuilt a time-calibrated phylogenetic tree for *Zenaida* using the mitochondrial sequences from Johnson and Clayton (2000) and estimated this colonization time as 3.51 MYA, suggesting this colonization may have occurred earlier than previously thought.

Darwin's Finches The ancestors of Darwin's finches also diverged from their sister group around two to three MYA, but the finches underwent one of the best-known cases of adaptive radiation (Sato et al. 2001; Grant and Grant 2008). Darwin's finches include 14 species in Galapagos and one species from Cocos Island. They form a monophyletic clade within the tanager family (Thraupidae) that is sister to a clade formed by the Dull-colored Grassquit (*Tiaris obscurus*) and the Sooty Grassquit (*Tiaris fuliginosus*) from South America (Sato et al. 2001; Burns et al. 2014). These phylogenies were built using mitochondrial and nuclear DNA sequences, and they revealed with high confidence that Darwin's finches are imbedded within a larger clade that includes mostly Caribbean endemics and a few South American species. This is consistent with the biogeographic inference from Burns et al. (2002) of a possible simultaneous dispersal from the Caribbean to both South America and Galapagos, forming a widely distributed clade that later evolved into a separate lineage in Galapagos.

Darwin's finches represent a shift in the rate of diversification within the tanager family, where species formation is faster in the genera of Darwin's finches than for any other tanager clade (Burns et al. 2014). This rapid diversification may have been an extrinsic result of geographic isolation and ecological release that the finches experienced when they colonized Galapagos (Burns et al. 2002, 2014). Finches were among the first terrestrial birds on the islands, perhaps along with the mockingbirds (Arbogast et al. 2006), and likely found a nearly empty niche space when they

arrived. Alternatively, their ancestors may have been genetically predisposed to radiating (intrinsic evolvability), possibly having a greater variety of regulatory genes controlling beak shape and size that were heritable (Burns et al. 2002, 2014). The adaptive radiation process of Darwin's finches also involved high rates of introgressive hybridization between species, which has allowed for the maintenance of high genetic diversity within species and provided abundant opportunity for natural selection to act (Grant et al. 2004, 2005; Petren et al. 2005). As a consequence, the different finch species proposed based on morphological characteristics are genetically very similar, and several of them (all tree and ground finches) do not directly correspond to monophyletic groups using mitochondrial genes and nuclear introns (Petren et al. 2005; Farrington et al. 2014) or whole-genome data (Lamichhaney et al. 2015).

The radiation of Darwin's finches does not seem to have followed the same pattern found for most of the lineages that speciated in Galapagos, the "progression rule," a pattern of older species on older (southeastern) islands and younger species on younger islands. Instead, most finch species have overlapping distributions, and both older and younger finch species are present on several islands, independent of when the islands formed. The diversification of Darwin's finches within Galapagos happened over a very short time, approximately 1.65 million years (Petren et al. 2005; Lamichhaney et al. 2015). This was characterized by the first lineage split giving rise to the Green Warbler Finch (*Certhidia olivacea*), which has the most basal position of the Darwin's finches (Petren et al. 2005; Burns et al. 2014). The Gray Warbler Finch (*Certhidia fusca*) diverged from the other finches soon after this first splitting event. At that time, the environment in Galapagos was warmer and wetter, with forests occupying most of the island landscape, and the warbler finches adapted to exploit small arthropods, fruits, nectar, and pollen from small flowers (Grant and Grant 2008). The diversification of tree and ground finches happened after the archipelago became more arid, with lower temperatures, less humidity, and the appearance of dry, open areas in the lowlands. These new environmental conditions arose around 1 million years ago and allowed the evolution of seed-eating and cactus-exploiting behaviors, directly influencing the radiation of finches (Grant and Grant 2008). The Cocos Island Finch (*Pinaroloxias inornata*) branched off from the phylogeny after the lineage splitting events that gave origin to warbler finches and, possibly, to the Vegetarian Finch (*Platyspiza crassirostris*), showing that the Cocos Island Finch derived from the radiation in Galapagos and not the opposite (Petren et al. 2005; Grant and Grant 2008; Lamichhaney et al. 2015).

Patterns for population genetic structure between islands vary among Darwin's finch species. High levels of gene flow were measured between populations within Santa Cruz Island, even in the presence of phenotypic divergence, suggesting natural selection rather than drift is responsible for morphological differences in these populations (*Geospiza fortis* [de Leon et al. 2010]; *G. fuliginosa* [Galligan et al. 2012]). Finches can also readily move between islands, and high levels of gene flow were detected between islands for most finch species (Petren et al. 2005; Farrington et al. 2014). Finch dispersal may be prompted by forest fires caused by volcanic eruption or by high population densities resulting from prolific breeding during El Niño years (Grant and Grant 2008). In contrast, warbler finches (*Certhidea* spp.),

the Sharp-beaked Ground Finch (*G. difficilis*), and the cactus finches (*G. scandens* and *G. conirostris*) showed significant differentiation among islands. For each of these species, genetic distances correlated to geographic distances between islands, suggesting dispersal and gene flow are reduced between the most distant islands (Petren et al. 2005). Another observed pattern for ground finches (*Geospiza* spp.) is that populations of two species that live in sympatry are genetically more similar than populations of the same two species that live in allopatry, a result of introgressive hybridization between sympatric species. Introgressive hybridization among finches in Galapagos is considered a central feature of their process of adaptive radiation (Grant et al. 2005; Petren et al. 2005).

Galapagos Mockingbirds Hybridization was probably not as important in the diversification process of the Galapagos mockingbirds, but it has also been detected in these species. Four species of Galapagos mockingbirds are recognized using traditional taxonomy: the Hood Mockingbird (*Mimus macdonaldi*) inhabiting Española, the San Cristóbal Mockingbird (*M. melanotis*) on the island of the same name, the Floreana Mockingbird (*M. trifasciatus*) on two islets adjacent to Floreana, and the Galápagos Mockingbird (*M. parvulus*) on the rest of the archipelago. This classification was only partially supported by genetic analyses of populations using mitochondrial DNA; these analyses suggested *M. parvulus* is polyphyletic, with the Genovesa population more similar to the other three species than to populations of *M. parvulus* from other islands (Arbogast et al. 2006; Štefka et al. 2011). Nietlisbach et al. (2013), however, revealed that the Genovesa population of *M. parvulus* possibly experienced introgressive hybridization of genes from the other mockingbird species in Galapagos. These authors, using microsatellites, nuclear, and mitochondrial DNA sequences, and morphology, supported the traditional classification of the four Galapagos mockingbird species, but also suggested that Genovesa birds are morphologically differentiated (Nietlisbach et al. 2013). Unlike Darwin's finches, Galapagos mockingbirds experience very little gene flow among islands. Their genetic diversity within populations is strongly correlated with island size, suggesting that drift plays an important role in the evolution and differentiation of these populations (Hoeck et al. 2010).

The closest living relative of all Galapagos mockingbirds is the Bahama Mockingbird (*M. gundlachii*), and other closely related species are found living in the Caribbean, Central America, and northern South America (Arbogast et al. 2006; Lovette et al. 2012). These phylogenetic relationships suggest a colonization history similar to that proposed for Darwin's finches (Burns et al. 2002), in which dispersal of mockingbird ancestors located in Central America and the Caribbean resulted in the colonization of Galapagos and a continental expansion in the Americas (Arbogast et al. 2006). Based on genetic divergence between the Bahama Mockingbird and the Galapagos mockingbirds, Arbogast et al. (2006) suggested that the lineage of Galapagos mockingbirds originated between 1.6 and 5.5 MYA, and the colonizers possibly arrived on the oldest islands of San Cristóbal or Española first. The species *M. melanotis* from San Cristóbal and *M. macdonaldi* from Española belong to one clade that split around 500,000 years

ago from the rest of the Galápagos mockingbirds (Nietlisbach et al. 2013). The next island colonization corresponded to the speciation event giving rise to the Floreana Mockingbird (*M. trifasciatus*), and only later were the central islands colonized by the ancestors of *M. parvulus*, the species with the widest distribution in the archipelago. The most recent colonization events within Galapagos occurred on the youngest islands of Isabela and Fernandina, showing that the mockingbird diversification process fits well with the progression rule (Nietlisbach et al. 2013). Differences between the species diversity of Darwin's finches and Galapagos mockingbirds may be attributed to the shorter time since diversification of mockingbirds (500,000 years) as opposed to the older diversification of finches that started 1.6 MYA (Nietlisbach et al. 2013). However, this difference could be more related to the generalist feeding habits of the mockingbirds (Arbogast et al. 2006; Nietlisbach et al. 2013).

Galapagos Hawk In contrast, the Galapagos Hawk (*Buteo galapagoensis*) is probably the youngest endemic bird in Galapagos, and still their differentiation from other *Buteo* species is remarkable. This is the only *Buteo* species that has cooperative polyandry, in which territorial reproductive groups are composed of one female and two or more males that equally contribute to siring and provisioning the chicks (Faaborg et al. 1995). Group size varies among islands, with the average number of males per territory ranging from one on Española (where only pairs were observed) up to five on Pinta (Bollmer et al. 2003). Several phylogenetic and phylogeographic studies have shown that the Galapagos Hawk forms a monophyletic group within the Swainson's Hawk, which breeds primarily in North America and migrates to South America, making the Swainson's Hawk a paraphyletic species (Riesing et al. 2003; Bollmer et al. 2006; Hull et al. 2008; Amaral et al. 2009). Bollmer et al. (2006) performed a phylogeographic study comparing Galapagos Hawks to Swainson's Hawks sampled in Argentina, using several mitochondrial genes. Based on the genetic divergence between these two species and a previously published diversification rate, the authors estimated that colonization of the Galapagos by *Buteo* hawks occurred less than 300,000 years ago. Amaral et al. (2009) built a phylogeny of buteonine hawks using a molecular clock based on biogeographical and fossil calibrations, and they similarly calculated the average age of the Galapagos Hawk to be 340,000 years. Ancestral state reconstructions of Buteoninae hawks showed that migratory behavior of Nearctic populations was important for diversification of *Buteo* species, including the colonization of Galapagos (Amaral et al. 2009).

Phylogeographic analyses of the Galapagos Hawks also revealed very low genetic diversity for the species and little differentiation among islands, with a typical pattern of quick and recent demographic expansion (Bollmer et al. 2006; Whiteman et al. 2007). The population from Española had the highest genetic distances from other island-populations, indicating that this may have been the first population to be isolated from the rest (Bollmer et al. 2006), possibly as a result of its peripheral position in the archipelago (see Petren et al. 2005). In contrast, faster evolving molecular markers (minisatellites and microsatellites) revealed strong

population genetic structuring among eight Galapagos islands, with very high global and pairwise F_{st} values, and where each island-population was assigned to its own genetic cluster (Bollmer et al. 2005; Koop et al. 2014). These results were more consistent with the significant morphological differentiation found among hawks from different islands (Bollmer et al. 2003). High genetic similarity detected within island-populations suggests that drift plays an important role in the distribution of genetic diversity within and among Galapagos Hawk populations (Bollmer et al. 2005), and it is possible that this species is in the early stages of lineage diversification within the archipelago.

2.2.2 *Two Flycatchers and One Warbler: Was There More Lineage Diversification in Galapagos?*

Three other lineages of terrestrial birds that colonized Galapagos—the Galapagos Flycatcher (*Myiarchus magnirostris*), the Vermilion Flycatcher (*Pyrocephalus rubinus nanus* and *P.r. dubius*), and the Yellow Warbler (*Setophaga petechia aureola*)—have not received as much attention as Darwin’s finches and the Galapagos mockingbirds. The Galapagos Flycatcher and the Yellow Warbler are distributed on all the main islands of the archipelago, except for the most northern ones, and they are found in all vegetation zones and elevations on the islands they inhabit (Jackson 1993). In contrast, the Vermilion Flycatcher is found mainly in the highlands and so is more or less restricted to larger islands that have higher elevations, although they may also occur on the coasts of smaller islands such as Pinzón and Marchena (Jackson 1993). They are frequently found in association with *Scalesia* vegetation and are seen much more rarely than the Galapagos Flycatcher and the warbler, suggesting that their population sizes are smaller. Recent phylogenetic studies have shown evidence that each of these three taxa is monophyletic in Galapagos, confirming that these lineages are independent of their continental counterparts (Chaves et al. 2012; Sari and Parker 2012; Carmi et al. 2016).

Galapagos Flycatcher Traditional taxonomy studies suggested that the sister species of the Galapagos Flycatcher was the Brown-crested Flycatcher (*Myiarchus tyrannulus*), which is distributed from the southern United States to Argentina and has several recognized subspecies (Lanyon 1960, 1978). Sari and Parker (2012) constructed a phylogenetic tree using a comprehensive sampling of species in the genus *Myiarchus*, including various subspecies of the Brown-crested Flycatcher. They calibrated the tree with a previously published genetic substitution rate (2.07% per million years for cytb; Weir and Schluter 2008). The authors recovered a monophyletic clade for the Galapagos Flycatcher and confirmed its sister relationship with a Brown-crested Flycatcher lineage distributed in Central America. Sari and Parker (2012) estimated the timing of the split between these two lineages to be approximately 850,000 years ago, which represents the maximum age for the Galapagos Flycatcher species. Analyses of mitochondrial DNA sequences from

Galapagos Flycatchers sampled on seven islands showed a pattern typical of recent population expansion, with little genetic structuring between pairs of islands (Sari and Parker 2012). However, the islands of Santa Cruz and Floreana were exceptions to this overall pattern; Galapagos Flycatcher populations on both of these islands were genetically differentiated from all the other island populations.

Yellow Warbler A very similar pattern was observed for Yellow Warbler populations from nine Galapagos Islands. Chaves et al. (2012) detected a genetic signal of recent population expansion in this subspecies of Yellow Warbler and found mitochondrial haplotypes exclusive to the islands of Floreana and Santa Cruz. The authors also used microsatellites to quantify the genetic structure of populations across islands and took morphological measurements of warblers from four islands: Isabela, San Cristóbal, Santa Cruz, and Santiago. While they found that warbler populations on the islands of San Cristóbal and Floreana were genetically differentiated from the other island-populations, the authors found no evidence of morphological differences among islands. A similar trend was detected in the Galapagos Flycatcher; a comparison of populations using microsatellites and morphological data revealed the population of San Cristóbal to be genetically, but not morphologically, differentiated from populations on other islands (Sari and Parker, unpublished data). With Española, San Cristóbal is one of the most southeastern islands in the archipelago, and its peripheral position may result in reduced gene flow to and from the more central islands.

A phylogenetic analysis placed the Yellow Warbler of Galapagos into a monophyletic clade that included yellow warblers from Cocos Island, located a few hundred miles northeast of Galapagos (Chaves et al. 2012). This clade likely originated in Central America, where its sister clade (including the subspecies *xanthotera* and *erithachorides*) is distributed, and the authors estimated these two clades diverged approximately 270,000 years ago (Chaves et al. 2012). Interestingly, even though the Galapagos Flycatcher likely colonized the archipelago 600,000 years before the Yellow Warbler, the two species still share a similar population structure. This may be due to both species having similar ecological requirements that have led them to respond in similar ways to geographic and climatic factors that influence gene flow and drift.

Vermilion Flycatcher Very little is known about the evolutionary history of the Vermilion Flycatcher in Galapagos. Two endemic Galapagos subspecies were proposed for the Vermilion Flycatcher based on morphological characteristics, *P. rubinus nanus* and *P. r. dubius*, the latter being present only on San Cristóbal Island (Jiménez-Uzcátegui et al. 2015). Species delimitation for these birds (as with others) is essential for their conservation. For example, the Vermilion Flycatcher population on San Cristóbal is thought to have gone extinct, which would represent the extinction of an endemic subspecies. To better understand evolutionary relationships in the Vermilion Flycatcher, Carmi et al. (2016) produced a phylogeny for *P. rubinus* (including most of its subspecies) using mitochondrial and nuclear DNA sequences. They also included historical museum samples from the San Cristóbal

population. The authors recovered a monophyletic clade composed of Vermilion Flycatchers from Galapagos that is sister to another monophyletic clade with all *P. rubinus* subspecies from the American continent. The continental and the Galapagos clades were estimated to have diverged about 1.15 MYA. Interestingly, the authors recovered three clades within Galapagos that were more than 2% divergent from each other. The first split among these clades corresponds to the San Cristóbal population, and the other two clades are sisters and correspond to a south/west (Floreaña, Isabela and Fernandina) versus north/central (all other islands) distribution (Carmi et al. 2016). This result is significant in the sense that it confirms one more instance of species diversification for Galapagos birds. The authors recommended that the “Galápagos forms [of the Vermilion Flycatcher] should be elevated to two full species”: *P. nanus* and *P. dubius* (Carmi et al. 2016). Unfortunately, this would mean that *P. dubius* may represent the first documented case of an endemic bird extinction in Galapagos.

2.2.3 *Cormorants and Penguins: Similar Distributions and Arrival Times, Different Population Structure*

Taxa on isolated islands often diverge from their continental congeners in an expected way referred to as the “island syndrome,” and the Flightless Cormorant (*Phalacrocorax harrisi*) and the Galapagos Penguin (*Spheniscus mendiculus*) represent extreme examples of this syndrome. The cormorant has atrophied wings and lost its ability to fly, while the penguin has adapted from a polar to a tropical environment, with cool waters and hot rocks. Their breeding colonies overlap along the coastlines of Isabela and Fernandina, but the penguin’s distribution also extends to small areas of Santiago and Floreaña Islands. Phylogenies have been proposed for both species with their related taxa, and there is evidence that both colonized Galapagos around the same time, two MYA.

Flightless Cormorant Kennedy et al. (2009) constructed a phylogeny for the genus *Phalacrocorax* using mitochondrial DNA sequences and found strong support for the Flightless Cormorant being sister to a clade containing the Double-crested (*P. auritus*) and the Neotropic (*P. brasilianus*) Cormorants. Double-crested Cormorants are common and widely distributed in North America and Cuba, and Neotropic Cormorants can be found all over the Neotropics, from Mexico to Argentina, and in the Caribbean. Therefore, the American continent seems to be the geographic origin for the Galapagos Flightless Cormorants. Using the percent of genetic divergence between the Flightless Cormorant and its sister clade along with previously published substitution rates, Kennedy et al. (2009) estimated the time of arrival to Galapagos as approximately two MYA. At that time, neither of the islands that the Flightless Cormorants inhabit today existed, as Fernandina and Isabela are estimated to be fewer than 300,000 years old. However, the island of Santa Cruz

could have been the center for their arrival and early establishment. Flightless Cormorants rely on upwelling waters for feeding, and around two MYA those were already available along the western coast of Santa Cruz. The formation of Isabela and then Fernandina likely impacted the local marine circulation, making the foraging grounds around Santa Cruz no longer suitable for the cormorants and forcing them to relocate to western islands in search of food (Kennedy et al. 2009).

Galapagos Penguin The Galapagos Penguin is also dependent on the upwelling for survival, and its establishment in Galapagos may have been similar to that of cormorants, except that today there are small populations of penguins on Floreana, which was also above-water when penguins likely arrived in Galapagos. Phylogenetic studies showed that the sister species of the Galapagos Penguin is the Peruvian or Humboldt Penguin (*Spheniscus humboldti*), so their ancestors most probably colonized Galapagos from South America (Baker et al. 2006; Subramanian et al. 2013). Baker et al. (2006) proposed a phylogeny for all extant penguins using a molecular clock calibrated with non-penguin fossils and suggested that the time for the split between the Galapagos Penguin and the Peruvian Penguin was about 4 MYA. Subramanian et al. (2013) constructed a penguin phylogeny using a larger number of nuclear introns, including all previously published penguin DNA sequences, and estimated that the common ancestor of all extant penguins dates to about half the time that was proposed by Baker et al. (2006), with the origin of the Galapagos Penguin occurring much later, about 1.9 MYA. This phylogeny was calibrated using several penguin-specific fossils, which allowed better estimates of evolutionary rates (Subramanian et al. 2013).

Population dynamics and migration between populations were shown to be very different in the two species. Nims et al. (2008) estimated genetic variability in Galapagos Penguins from five locations on Isabela, Fernandina, and Santiago using microsatellites. They found low genetic diversity for the species and no evidence of genetic differentiation between colonies within or between islands. In addition, high levels of gene flow between populations were found, showing that penguins have no barriers to movement throughout their range (Nims et al. 2008). Galapagos Cormorants, on the other hand, seem to have barriers to dispersal, even between very short geographic distances and especially across open water (Duffie et al. 2009). Six colonies from Isabela and three from Fernandina were analyzed using microsatellites, and most of the pairwise genetic comparisons both within and between islands showed significant structure. Cormorant samples clustered into two genetic groups corresponding to Isabela and Fernandina. Also, genetic distances between colonies were positively correlated with coastline geographic distances, but not with shortest swimming distances, indicating that the ocean is a significant barrier for movement of cormorants (Duffie et al. 2009). These differences in population dynamics between penguins and cormorants have important implications for their conservation. For example, cormorants from different islands need to be treated as different management units, but penguins from all around the archipelago may represent one single evolutionary unit.

2.2.4 *Seabirds with a Global Range and Their Populations in Galapagos*

The Galapagos Islands have extensive coastlines and are surrounded by thousands of miles of open ocean, representing an ideal space for breeding populations of numerous seabird species. Seabirds are known for their strong flight and dispersal capabilities (they can travel hundreds of miles while foraging), broad distributions, and success in reaching and establishing breeding colonies on remote islands. Some of the seabird species found in Galapagos have been studied in a larger geographical context, extending beyond the Galapagos archipelago. These studies revealed that, while there is evidence for gene flow between boobies (*Sula* spp.) of Galapagos and those of other locations in the Pacific (Friesen et al. 2002; Steeves et al. 2003; Morris-Pocock et al. 2010; Taylor et al. 2011), the Band-rumped Storm Petrel (*Oceanodroma castro*; Smith et al. 2007), the Magnificent Frigatebird (*Fregata magnificens*; Hailer et al. 2011), and the Galapagos Petrel (*Pterodroma phaeopygia*; Welch et al. 2011) are likely genetically isolated in Galapagos. None of the seabird taxa found in Galapagos have radiated into multiple lineages, and research has shown that they are closely related to populations and species located in the Pacific Ocean.

Storm Petrel The Band-rumped Storm Petrel (also called the Madeiran Storm Petrel) has a widespread tropical and sub-tropical distribution in both the Atlantic and Pacific Oceans, and individuals are thought to return to their place of birth to breed (a phenomenon known as philopatry). Smith et al. (2007) examined global patterns of mitochondrial DNA variation in 386 adult band-rumped storm petrels in several Atlantic and Pacific populations, including the islet of Plaza Norte in Galapagos. They found that individuals from Galapagos were genetically distinct from all other locations, sharing no haplotypes with other populations. Because the Galapagos population was reciprocally monophyletic, Smith et al. (2007) used the percent of genetic divergence between populations and a previously published sequence divergence rate (21% per million years for mitochondrial control region; Quinn 1992) to estimate divergence time. The analysis revealed that band-rumped storm petrels from Galapagos have been isolated for about 150,000 to 190,000 years and are more closely related to other Pacific populations than to Atlantic populations. Based on these results, Smith et al. (2007) suggested that the Galapagos populations “may qualify as phylogenetic and biological species” and that their species status should be reconsidered, with the caveat that analyses of nuclear DNA sequences were also necessary. If this taxonomic suggestion is accepted, it will add one more endemic species to the Galapagos bird community. This decision, however, should be considered with caution, because the individuals used in the aforementioned study were all from a single island in Galapagos. Band-rumped Storm Petrels breed on nine other Galapagos islands (Jackson 1993), where different haplotypes could potentially exist. Regardless of the species’ taxonomic status, this colonization represents the most recent of all native Galapagos species to date.

Magnificent Frigatebird A phylogeographic approach was also used by Hailer et al. (2011) to study populations of the Magnificent Frigatebird from the Galapagos island of North Seymour and several locations along the Pacific coast of Central and North America and the Caribbean. Similar to what was found for the Band-rumped Storm Petrel, Galapagos magnificent frigatebirds shared no mitochondrial haplotypes (ATP6, cytochrome b, and ND2) with other populations. Also, pairwise Φ_{st} values were significant and larger than 0.90 for all comparisons between Galapagos and other populations. This same pattern of differentiation was recovered in analyses using microsatellites and one nuclear intron (Hailer et al. 2011). Using a phylogenetic tree calibrated with a previously published substitution rate and also with a geological event, the authors estimated that the North Seymour (Galapagos) population diverged from other populations approximately 247,000 years ago. Additionally, Hailer et al. (2011) detected morphological differences between Galapagos and non-Galapagos populations, in which frigatebirds from Galapagos were significantly larger. Furthermore, these authors hypothesized that a behavioral mechanism could be involved in the evolutionary isolation of the magnificent frigatebirds in Galapagos by, for example, isolating their feeding range or increasing their selectiveness to avoid nonspecific or non-local matings. While no taxonomic recommendation was made, Hailer et al. (2011) did propose that the Galapagos population be treated as a separate evolutionary and management unit. Jiménez-Uzcátegui et al. (2015) took it a step further and suggested treating the Galapagos population as the endemic subspecies *magnificens*. Aside from the Galapagos population, the other Pacific and Caribbean populations were not genetically different from each other and inferences about the geographic origin of the Galapagos population were not possible.

Galapagos Petrel The Galapagos Petrel and the Hawaiian Petrel are morphologically very similar and were considered conspecifics until 2002, when they were elevated to species status based on differences in breeding phenology, song, and a single allozyme locus (see Welch et al. 2011). This taxonomic change was likely important for their conservation, since the Galapagos species is now considered critically endangered (Bird Life International 2016). The timing of the genetic differentiation of these two species was recently explored using mitochondrial and nuclear genetic markers (Welch et al. 2011). The results suggested that the two species diverged approximately 550,000 years ago, but nuclear markers indicate that this divergence occurred with incomplete lineage sorting (Welch et al. 2011). Within Galapagos, little gene flow was detected at either microsatellites or sequence data among populations on the five islands where Galapagos petrels breed (Friesen et al. 2006; Welch et al. 2011). Furthermore, microsatellite data revealed that these island-populations represent three genetic clusters: (1) Floreana, (2) Santa Cruz, and (3) Santiago and Isabela. San Cristóbal has a mixture of individuals from all three clusters. Based on these data, Friesen et al. (2006) suggested that Floreana, Santa Cruz, San Cristóbal, and Santiago all “should be regarded as separate genetic management” units for conservation purposes.

Boobies The three booby species (family Sulidae) of Galapagos have been found to be genetically most similar to conspecific populations from other parts of the Pacific. The Red-footed Booby (*Sula sula*; Syn.: *Sula sula websteri*) population from Genovesa Island shares no mitochondrial haplotypes with populations from the Caribbean, Atlantic, and Indian oceans. However, this population is genetically indistinguishable from other Pacific populations of *Sula sula rubripes* (Steeves et al. 2003; Morris-Pocock et al. 2010), suggesting a confusing taxonomic classification for subspecies. Similarly, the Blue-footed Booby (*Sula nebouxii*) populations from Galapagos are considered an endemic subspecies (*S. n. excisa*), but Taylor et al. (2011) found that Galapagos populations are not genetically different from populations sampled on other islands off the coasts of Ecuador and Peru. They also found no genetic structuring among Blue-footed Boobies from the islands of North Seymour, Champion and Española islands in Galapagos, suggesting substantial movement of these birds across the archipelago. Finally, the Nazca Booby (*Sula granti*) populations from Galapagos share haplotypes with populations of other Pacific islands (Friesen et al. 2002; Patterson et al. 2011). Levin and Parker (2012) found only limited gene flow among islands in Galapagos. An estimate for the arrival time of Nazca Boobies to Galapagos has not been calculated, but it cannot be older than the ages estimated for the formation of the species, which is between 700,000 (Friesen et al. 2002) and 1.1 million (Patterson et al. 2011) years ago.

2.3 Species Introduced by Humans

Non-ephemeral human settlements in Galapagos originated in the 1800s, but whalers and buccaneers were regularly visiting the islands beforehand. These visitors introduced exotic species to the islands both by accident, as in the case of rats from their ships, and on purpose, as in the case of domestic goats released onto the islands as a food source for future trips (Jackson 1993). Exotic species probably represent the greatest threat to the Galapagos terrestrial ecosystem, as they can disturb the equilibrium of the endemic species community in several different ways. Humans have introduced around 40 terrestrial vertebrate species to Galapagos, including 12 bird species (Phillips et al. 2012b). Four bird species are domesticated and cultivated for human use: the chicken, duck, goose, and turkey (Jiménez-Uzcátegui et al. 2015). Chickens, ducks, and turkeys have been kept in domestication on Galapagos since 1937, and they are found in human settlements on the islands of Santa Cruz, Floreana, San Cristóbal and Isabela (Phillips et al. 2012b). Other species introductions are considered accidental, namely the Quail, Guinea Fowl, Peacock, Saffron Finch, Red-masked Parakeet, Rock Pigeon, Smooth-billed Ani, and Cattle Egret.

Rock pigeons (*Columbia livea*) were introduced to Galapagos in the 1970s and established free populations in the islands of Santa Cruz, San Cristóbal, and Isabela, following the failed project of a loft (Phillips et al. 2012b). Rock pigeons reached large populations in the 2000s and their potential for transmission of several pathogens and parasites was considered a concern for humans and for the naive avifauna in

Galapagos. Therefore, since 2006 this introduced species has been extirpated from the islands, after a seven-year eradication campaign (Phillips et al. 2012a). The Smooth-billed Ani (*Crotophaga ani*) and Cattle Egret (*Bubulcus ibis*) have become naturalized and have wild populations on most of the islands (Phillips et al. 2012b). The Smooth-billed Ani likely was introduced by farmers in the 1960s to help control ticks from cattle. They are most common in the agricultural zone on Santa Cruz Island, but they have invaded several other islands. Cattle egrets have spread freely around the world for the past two centuries following the expansion of human activities, and their presence in Galapagos may be an indirect result of cattle brought by humans (Jackson 1993). This illustrates how human activities can modify a community's species composition even when they are not directly introducing or eliminating species.

2.4 Concluding Remarks

The native Galapagos avifauna is composed of species with their own idiosyncratic colonization histories, in which both colonization times and geographic origins vary greatly. These species also vary in their diversification patterns post-colonization, with factors such as life history traits, island geology, and trade winds affecting the genetic patterns described. The majority of these bird lineages have been evolving in relative isolation for thousands or millions of years and as a result, they may not have the necessary defenses against novel pathogens: either because they lost their immunological capacity (see Chap. 4) or their ability to move and escape these pathogens and parasites (see Chap. 5). Therefore, among the threats to the native Galapagos bird fauna, the introduction of novel pathogens was considered one of the most serious for their conservation (Parker et al. 2006). A diversity of pathogens and parasites is found in Galapagos, and they reached the islands both through natural colonization and human activities (see Chap. 3). One of the main threats the 12 exotic bird species may represent to the native Galapagos avifauna is through the introduction and transmission of pathogens. Continued research into colonization histories and evolutionary units of native lineages will aid our understanding of host-parasite interactions and better inform conservation management decisions.

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