Social and Ecological Interactions in the Galapagos Islands

Patricia G. Parker *Editor*

Disease Ecology

Galapagos Birds and their Parasites

Springer

Social and Ecological Interactions in the Galapagos Islands

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Series Preface

Galapagos Book Series, "*Social and Ecological Sustainability in the Galapagos Islands*"

In May 2011, the University of North Carolina (UNC) at Chapel Hill, USA, and the Universidad San Francisco de Quito (USFQ), Ecuador, jointly dedicated the Galapagos Science Center, an education, research, and community outreach facility on San Cristobal Island in the Galapagos Archipelago of Ecuador. The building dedication was the culmination of an emerging partnership between UNC and USFQ that began several years earlier through a 2006 invitation to Carlos Mena and Steve Walsh to assist the Galapagos National Park and the Nature Conservancy in a remote sensing assessment of land cover/land use change throughout the archipelago. Leveraging related work in the Ecuadorian Amazon, Carlos Mena (USFQ Professor of Life and Environmental Sciences) and Steve Walsh (UNC Lyle V. Jones Distinguished Professor of Geography), Co-Directors of the Galapagos Science Center, and Brian Frizzelle of the UNC Carolina Population Center traveled throughout the islands using pre-processed satellite imagery and spectral and geospatial equipment to validate preliminary analyses of the Galapagos with a focus on invasive plant species. Since that project, Mena and Walsh have continued to regularly engage the Galapagos Islands, coordinating research conducted at the Galapagos Science Center by faculty, staff, and students from both campuses as well as by collaborating scientists from institutions around the globe who together seek to understand the social, terrestrial, and marine subsystems in the Galapagos Islands and their linked and integrative effects. Now with nearly 50 permitted Park projects operating at the Galapagos Science Center and a diversity of scientific topics being studied using a host of theories and practices, innovative work continues in an assortment of compelling vital ways. The state-of-the-art facilities at the Galapagos Science Center include nearly 20,000 square feet of space that supports four laboratories (i.e., Microbiology and Genetics, Terrestrial Ecology, Marine Ecology, and Geospatial Modeling and Analysis), operated through a permanent administrative and technical staff, to support science, conservation, and sustainability in the Galapagos Islands. In addition, students enroll in classes taught by UNC and USFQ faculty as well as conduct research to complete their undergraduate honors theses, graduate theses, and doctoral dissertations. Several scientists at the Galapagos Science Center engage the community on topics including water and pathogens, nutrition and public health, and tourism and community development.

From these beginnings and with the general intention of developing a Galapagos Book Series to document our scientific findings, highlight special needs, and describe novel approaches to addressing special social-ecological challenges to the conservation and sustainability of the Galapagos Islands, the Springer Book Series was launched through its inaugural book, *Science and Conservation in the Galapagos Islands, Frameworks & Perspectives*, edited by Steve Walsh and Carlos Mena and published by Springer in 2013. The Series has continued to expand, with books on Evolution, the Galapagos Marine Reserve, and Darwin and Darwinism. Now with considerable pleasure we welcome, *Disease Ecology of Galapagos Birds*, edited by Patricia Parker. This book addresses important elements of the story and condition of birds in the Galapagos Islands, with a central focus on a collection of interesting and vital topics—colonization, pathogens, hosts and parasites, the special circumstances that have led to evolutionary change of birds in the Galapagos Islands, and so much more.

The general goal of the Galapagos Book Series is to examine topics that are important in the Galapagos Islands, but also vital to island ecosystems around the globe. Increasingly, viewing islands as a coupled human-natural system offers a more holistic perspective for framing the many challenges to island conservation and sustainability, but the perspective also acknowledges the important context of history, human population, migration of plants, animals, and people, development, disturbances, and the evolution and adaptation of species (human and otherwise) on islands to changing social and ecological circumstances. *Disease Ecology of Galapagos Birds* makes considerable contributions to this perspective and offers a rich understanding of birds in the Galapagos Islands and the forces and circumstances of change and adaptation. Parker has assembled an expert set of authors to write vibrant chapters that are important as stand-alone statements of bird ecology of the Galapagos Islands, but are also woven into a collective statement that offers new insights, interpretations, and conclusions about Galapagos Birds.

Chapel Hill, NC, USA Stephen J. Walsh
Quito, Ecuador Carlos F. Mena

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Chapter 1
Introduction and Overview

Patricia G. Parker

Abstract The Galapagos Islands sit almost 1000 km west of Ecuador in the waters of the eastern equatorial Pacific. We have studied the birds there, most of which are endemic, and their parasites and pathogens, since 2001. Here I introduce the structure of this book, with sections on (1) the arrival of avian lineages and pathogens; (2) what commonly happens in new island populations once established, and the consequences for their now-isolated lineages; (3) how new host-parasite relationships are formed; (4) how pathogens spread once established; and (5) the rewards and challenges of attempting to understand disease threats with international teams. The sequential structure is intentional, and the author teams for individual chapters were invited because of their expertise on their topic, but most had not worked together before. Several teams wandered slightly away from their invited topics to present a broader context, but others did not. Some teams adhered closely to their own work, and others offered more comprehensive reviews on their topics. This book thus contains a mixture of voices and perspectives appropriate for such a complex topic.

Keywords Wildlife disease • Disease ecology • Hosts and pathogens

1.1 General Introduction: Galapagos and Wildlife Diseases

The Galapagos Archipelago straddles the equator in the eastern Pacific Ocean, almost 1000 km off the coast of Ecuador. The archipelago includes 13 major islands, numerous smaller satellite islands, and many more even smaller islets. People live on only four of the islands (Santa Cruz, San Cristobal, Isabela, and Floreana), and the others (plus the large majority of the surface of the four inhabited islands) are

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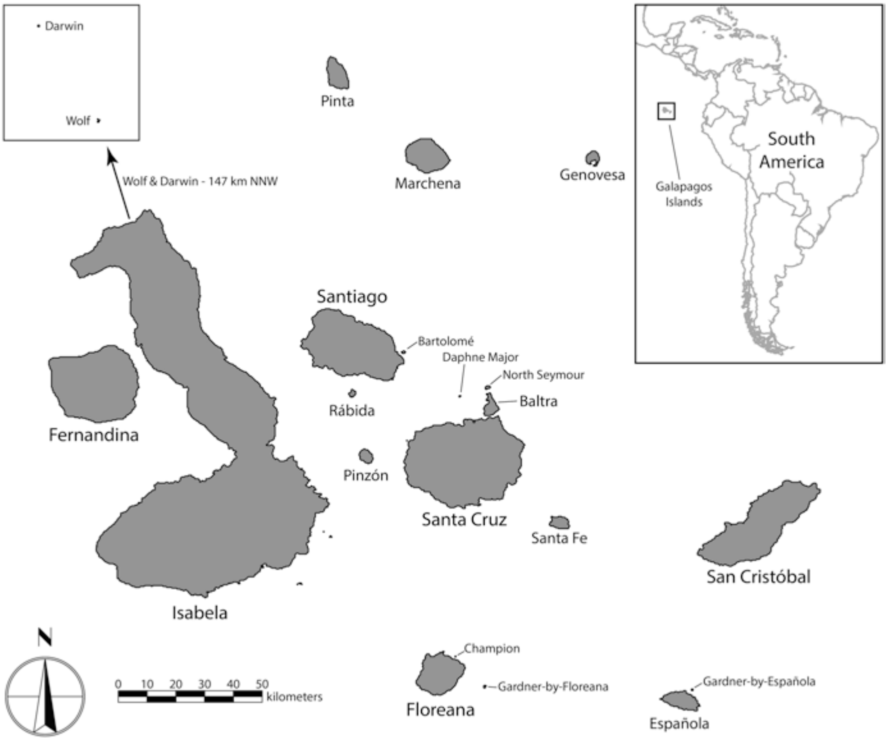

Fig. 1.1 Map of the Galapagos Islands. All of the islands labeled have been visited at least twice in our avian disease survey, including Darwin and Wolf. Some islands (e.g., Santiago, Santa Cruz, Isabela) are visited annually. Human populations occur on Santa Cruz, Isabela (far southern coast), San Cristobal, and Floreana. Original map prepared by Richard Swagel

protected as the Galapagos National Park by the government of Ecuador (Fig. 1.1). The wildlife on the Galapagos Islands today represents one of the best-preserved wild communities of plants and animals in the world, owing to the location of the islands in the eastern Pacific Ocean at the intersection of major currents, the commitment by Ecuador for the vast majority of the area to be left undeveloped, and the protection provided by the Galapagos National Park. Most of the animal species in Galapagos are endemic, occurring nowhere else. But they are descendants of ancestors that colonized earlier, and then, isolated from their mainland origins, evolved into forms that are recognized as distinct today. It is estimated that most of the original island fauna known to have occurred on the archipelago still persist in wild populations on the islands today, and all of the endemic bird species ever known to have occurred there are still present, with one possible exception.

This single possible extinction comes in the form of a vermilion flycatcher population now missing from the island of San Cristobal; before its disappearance, this population had been recognized as a sub-species (*Pyrocephalus rubinus dubius*), but was more recently determined, through a retrospective analysis of museum samples, to have been genetically distinct from forms on other islands, at a level considered deserving of species status (Carmi et al. 2016). The cause(s) of its disappearance are unknown. It is possible that more detailed genetic studies on island populations will reveal that other past and ongoing disappearances of what are now thought to be island populations actually represent extinctions of genetically distinct island forms, perhaps also distinct at the species level.

In 2000, the first international workshop on pathogens as threats to Galapagos birds was held at Princeton University, with participation and sponsorship by personnel from the Galapagos National Park as well as the Charles Darwin Foundation (CDF). The CDF is an international science advisory group that runs the Charles Darwin Research Station, located a 5-min walk from the headquarters of the Galapagos National Park outside of the town of Puerto Ayora on the island of Santa Cruz, Galapagos. The workshop resulted in an important publication (Wikelski et al. 2004) that summarized the scant knowledge of avian pathogens in Galapagos at that time, and the threats that diseases had posed to other island avian fauna, focusing particularly on the Hawaiian example, where dozens of species of endemic honeycreepers (Drepaniidae) are now extinct in one of the best-documented examples of extinction due to disease (e.g., van Riper et al. 1986, Atkinson and LaPointe 2009). Today, owing to several focused efforts, the CDF Checklist of Galapagos animals includes a section on Pathogens and Parasites listing 208 identified forms that include ectoparasites, endoparasites, viruses, and bacteria (Deem et al. 2014). Many of these are best known from extensive work with Galapagos birds, much of which is summarized in this volume.

Since 2001, many of the authors in this book have been part of a four-institution partnership investigating the threats posed by pathogens to Galapagos avifauna. The partner institutions are two from Galapagos and two from St. Louis, Missouri: (1) The Galapagos National Park, the agency primarily responsible for managing and protecting wildlife populations in Galapagos; (2) The Charles Darwin Foundation, an international science advisory group that runs the Charles Darwin Research Station on the islands; (3) The University of Missouri – St. Louis, with science strengths in tropical ecology, conservation, and genetic studies; and (4) The Saint Louis Zoo, with an institutional commitment to wildlife conservation and a veterinary staff whose charge goes beyond maintaining the health of their captive populations, to include significant field time to understand disease threats of wild populations. This is just one of several such collaborative efforts to address this challenge, and other authors in this book collaborated with that core group or had mounted similar collaborative efforts.

To date, we have surveyed bird populations of 26 Galapagos endemic bird species on all major islands (each island at least twice and some every year) and several smaller islets, published more than 100 papers and book chapters on our discoveries and growing understanding of pathogens in Galapagos birds, and awarded 26 graduate degrees (MS and PhD) associated with this work. Those degree recipients came to UMSL from seven different countries and graduates have returned to academic and conservation positions in their home countries or elsewhere. Collectively, we have identified multiple parasites that include viruses, bacteria, ectoparasites, and protozoan parasites. We have described and named previously undescribed species in some parasite groups.

1.2 Categories of Pathogens Found

In order to assess the levels of threat posed by the different pathogens, we begin by grouping them based on their histories on the islands, into:

1.2.1 Co-colonizers

Some parasites co-colonized with the ancestral colonizing bird lineages that have evolved into forms that are now recognized as Galapagos avian endemics. For example, when the ancestral migrating Swainson's Hawks (*Buteo swainsoni*) were blown off course and colonized the Galapagos Islands almost 300,000 years ago (Bollmer et al. 2006, Hull et al. 2008), some of those colonizing individuals had lice, just like the migrating Swainson's Hawks today have lice. Those lice co-colonized the archipelago with their hosts. The host hawk populations have since diverged into island-specific genetic forms and their lice have followed along, particularly those that are firmly latched onto feathers (Whiteman et al. 2007, Koop et al. 2014). These relationships continue to be interesting as examples of host-parasite evolutionary patterns that are interconnected and interdependent. But because of their long-established relationship, we do not have concerns about severe health impact stemming from lice, beyond the expected associations with age and breeding status (Whiteman and Parker 2004).

1.2.2 Host Switches

Some parasites or pathogens came in with one host lineage and have since "jumped" to a naive host lineage on the islands (or conversely, the parasite resided already on the islands when a new colonist arrived and became infected). A new colonizing host lineage may import parasites with which the colonizing host has a co-adapted relationship, as described in the previous category (1). If the "new" parasites are transmitted directly (i.e., can move independently to a new host), they may find novel (from the perspective of the parasite) hosts waiting for them in the form of previously colonized host lineages of other species. If the "new" parasites require specific vectors for transmission, as is the case with Haemosporidian blood parasites, for example, the availability of suitable vectors may determine whether that parasite can find new hosts on the islands, or indeed whether they can continue to be transmitted at all, even on the same host. A colonizing host lineage whose parasite is unable to be transmitted due to the absence of an essential appropriate vector on the islands will not transmit it, even to close associates. But if a suitable vector is present, the parasite may be transmitted to novel hosts where it may or may not be transmissible further, depending on its ability to adapt to the new host and the tolerance of that host. This relationship may happen in the other direction as well: a colonizing avian host lineage may encounter well-established parasite communities already on the islands that were not present in the colonizing bird's place of origin. In this case, the parasite's establishment on the islands has already taken place, and the new avian colonist will grapple with this in addition to the other challenges faced by colonists in a new environment.

1.2.3 Recent Arrivals

The final group includes parasites and pathogens that are more recent arrivals, likely connected in some way with human development and travel. The resident human population on the islands is between 25,000 and 30,000, split unevenly among the four human-inhabited islands. These residents fly back and forth to the mainland for much essential medical care and often for educational opportunities beyond those available on the islands. The number of residents exceeds the capacity of the agricultural zones on the four inhabited islands to provide for them, and multiple weekly supply boats make the journey carrying food and other supplies needed by the resident population. These conveyances can bring insects and pathogens, as can the fresh food that is being shipped. Pets and domestic livestock live on the inhabited islands with humans, and they are sources of pathogens as well. We would usually suspect that co-colonizing hosts and parasites in group (Sect. 1.2.1) are of less concern as we assume some level of reciprocal adaptation that has permitted this partnership to persist. This presumption of low pathogenicity in this group is strengthened by the fact that the natural colonist that founded the new Galapagos avian lineage was able to make the trip and establish in a new environment while infected. It is the group of most recently arrived parasites and pathogens in group (Sect. 1.2.3) that is most worrisome, particularly when the host infected by a new pathogen on the islands has been without exposure to parasites within that group for thousands of generations.

To place host/parasite combinations within this framework, we need to know the colonizing histories of the avian host lineages as well as their parasites and pathogens. We need to know the transmission dynamics of the parasite or pathogen and, if they require an agent or vector, we need to understand the ecology of that vector on the islands; those patterns may be different than the ancestral vector and host relationships elsewhere. Our goal in this book is to examine the fundamental processes underlying the colonization of hosts and pathogens, the establishment of new host-parasite relationships, and the potential conservation impact of parasites in island ecosystems.

1.3 Organization of This Book

This book is organized specifically to explore the steps in the process of establishing, maintaining, and often changing host and parasite relationships on islands. The sections are envisioned as a sequential exploration of these processes, in terms of the technical approaches used and the understanding that has emerged from those applications. Although the overarching theme is to present a way of understanding disease ecology on islands, owing to this sequential structure, there are some chapters that have barely a mention of a pathogen because they focus on other steps in the process of getting compatible hosts and parasites/pathogens into the same place at the same time. The overarching structure is not intended as a series of examples or stand-alone studies, although you will find plenty of examples in each of the chapters focused on points along the sequence of colonization by hosts and parasites, adaptation of each to their new homes, the potential for new host and parasite relationships, and a final section on how these understandings can inform conservation and management decisions.

1.3.1 Part I: Colonization of Islands by Hosts and Parasites

We start by trying to understand how the bird lineages themselves arrived, over what time period and how this is estimated. In Chap. 2, Sari and Bollmer explain how we know (or estimate) when the colonizations occurred that led to today's endemic Galapagos lineages, using phylogenetic approaches that calculate the genetic distance between the Galapagos endemic forms and their closest mainland relatives. That there is no established lineage on Galapagos today that is thought to have involved more than one successful colonization testifies to the challenges faced by colonists; even the famous finch radiation to 13 species, and the mockingbirds now considered four species isolated on different islands, arose from just two successful colonizations (one finch and one mockingbird). Just think how many unsuccessful colonists there must have been (and continue to be)! Sari and Bollmer also describe the location of the Galapagos archipelago at the intersection of major ocean currents and trade winds that strongly influence climate in Galapagos, and favor colonization from certain directions (and make return movement difficult).

Chapter 3 treats the same question for pathogens, parasites, vectors. The approaches used are sometimes different here, because these creatures are often not multicellular, except for the arthropod vectors, which can be examined using much the same approaches as those used to understand the colonization of avian hosts in Chap. 2, catching whole animals and comparing them genetically to mainland relatives. In Chap. 3, Bataille, Levin, and Sari explain what is known about the arrival of pathogens and vectors, and we see that many or most came with a successfully colonizing host lineage, with migratory birds stopping over on the islands en route, or with humans. Of the three mosquito species present, only one colonized naturally prior to human inhabitation. Vectors that occur primarily in ectoparasitic relationships with birds are both parasites themselves and often vectors for other, smaller parasitic organisms, often protists, that require passage through the ectoparasite and through that parasite's vertebrate host. The layers of intertwined parasitic relationships of Hippoboscid flies and Haemosporidian blood parasites present a challenge that is beginning to be understood. The arrival of viruses and bacteria is more challenging still, since their presence is often determined serologically, testing for the presence in a bird's blood of antibodies against that pathogen; a bird that is seropositive has been exposed to that pathogen at some earlier time. But we do not have historic blood samples for Galapagos birds prior to 2001, and so cannot test historically except for pathogens like the poxvirus that leaves characteristic lesions on the skin of museum specimens that can be tested for diagnostic criteria by histopathology and genetic tests. Understanding the arrival time and routes for pathogens and vectors is one of the most vexing challenges in disease ecology, and Bataille, Levin, and Sari pull together what can be understood.

1.3.2 Part II: Island Syndromes

Once a host lineage arrives, assuming it colonizes successfully and is able to reproduce, it begins to change. Bollmer and Nims explore in Chap. 4 the various genetic consequences of island colonization for the vertebrate host. In most cases, the ancestral lineage was highly mobile, and it seems a small band of migrants that normally do not fly over water, like Buteo hawks that migrate between continents by flying over land, was blown off course and was lucky to land in Galapagos, with at least one male and one female. Whatever the founding party size, it cannot possibly contain all of the genetic diversity available in the ancestral mainland population; nowhere is there a greater signature of genetic drift than in perpetually small island populations. The environment is likely distinctly different from that of the colonizing lineage's starting point, so selection will be strong as well, and the combination of selection and drift results in often shockingly low levels of genetic diversity, and sets the stage for very rapid change of morphology and physiology in island birds. These same forces act on functional genetic diversity as well, such as loci like the Major Histocompatibility Complex associated with immune response. These combined forces may leave island populations vulnerable to the arrival of pathogens that are novel to them. These patterns are well studied in several bird taxa in Galapagos.

In Chap. 5, Duffy and Vargas revisit this general pattern and take it further to explore other characteristics often associated with the "island syndrome." In this chapter, we will learn about some of the patterns that the depauperate genetic diversity and perpetually small populations on islands can produce that are common across islands, not just Galapagos. Since there are few predators (large carnivores are typically not present on isolated oceanic islands), being larger or more sedentary or less agile is less costly than in continental communities where escaping predation is important. Sedentariness in island fauna often develops quickly from a highly mobile colonizing ancestor. Flightlessness in highly mobile migratory bird lineages has evolved repeatedly on isolated islands, from unique species of flightless rails on several different islands or archipelagos, flightless ducks on others, and the flightless cormorant on Galapagos. Similarly, insular gigantism is part of the island syndrome; Galapagos examples include the famous Galapagos giant tortoises, and the less-appreciated Galapagos giant centipede.

1.3.3 Part III: Host-Switching

Once both host and parasite lineages have arrived, the receiving community is very different from what either experienced in their ancestral mainland community. Colonizing host populations are inherently small at founding, and will likely remain small compared to continental populations of relatives. A parasite that spends part of its life independently, off a host, will find populations of other already-present host species more abundant than the host species they arrived with. Jaramillo and Rivera-Parra, in Chap. 6, discuss the first step in this process of "trying out" new hosts, which can include a number of processes that collectively we label as "spillover." Parasites that require complex co-adapted interactions with hosts in order to complete their life cycle may infect a new host but not complete their life cycle in that host until they have become co-adapted, which may take many failed attempts, or may never happen. But if there is a sufficient reservoir of competent hosts that permit the completion of the parasite's life cycle, these trials with not-yet-competent hosts may continue until the parasite and new host become compatible. In either case, whether the parasite can complete its life cycle or not, the new host may suffer reduced fitness because of the infection, and conservation managers would be wise to monitor spillover infections. Jaramillo and Rivera-Parra have studied the ecological circumstances under which spillover is likely and when it is likely to succeed.

In Chap. 7, Santiago-Alarcon and Merkel discuss cases in which the relationship with the new host has succeeded, in the sense that the parasite completes its life cycle in the new host, and the new host survives the infection. If the parasites in the new host are isolated from those in the former host because of the transmission dynamics of the parasite or the community structure, these may represent true host switches and establish an independent parasite lineage that may lead to speciation of the parasite. These authors explore two Galapagos examples in some detail, the Haemosporidian blood parasite *Haemoproteus multipigmentatus* infecting the endemic Galapagos dove (*Zenaida galapagoensis*), thought to have arrived on the islands with introduced rock doves (pigeons: *Columba livia*) and jumped from them to the endemic dove, the only other columbiform bird present on the islands, an example from Sect. 1.2.2 of this chapter. The second example focuses on a microfilarid nematode discovered in both Galapagos penguins (*Spheniscus mendiculus*) and Galapagos flightless cormorants (*Phalacrocorax harrisi*). In both cases, we will learn the procedures involved in drawing conclusions and the remaining uncertainty in understanding the direction of the "jump."

1.3.4 Part IV: The Spread of Pathogens

In Chap. 8, Levin and Bataille explore the processes by which parasites and pathogens spread geographically among islands in an archipelago. For a parasite that is a specialist on a particular host species, its spread may depend in part on the movement patterns of that host. Levin and Bataille use the genetic structure of hosts as an index to their movement, assuming that movement of genes reflects individual movements to some degree. In this scenario, highly sedentary hosts with genetically distinct subpopulations are predicted to spread their taxon-specific parasites less efficiently (if at all) than hosts with significant gene flow among island populations. Some pathogens and vectors are capable of environmental movement off the host; Levin and Bataille present examples of mosquitoes that have been taken in aerial samples above boats, flying over open water. Life stages of some pathogens may be moved passively in the environment; the transmissive stage of *Toxoplasma gondii* consists of oocysts that are shed in the feces of feline definitive hosts. These oocysts are notoriously robust and may survive off the host for long periods in certain environments; and may even be moved by water currents in Galapagos to islands where there are no cats; this possibility is being explored.

Of all pathogens known to occur today on the Galapagos Islands, the free-living ectoparasitic fly *Philornis downsii* is one of the most harmful and best-studied. Its females lay their eggs in the materials of bird nests, and the larvae migrate to the nestlings, where they may enter nares or ears or other orifices to feed on body tissues, and later feed from nesting substrate directly on nestlings' ventral surfaces. They leave the nestlings to pupate in the nesting materials and then are thought to be non-parasitic as adults, feeding on fruits and plant material. Infection rate is very high in passerine bird nests on some islands, and mortality of nestlings is high as well. Its arrival and spread, and other aspects of its ecology, have been studied extensively, and in Chap. 9, Fessl, Heimpel, and Causton summarize their own work and that of others on this parasite. It is the sole exception to my claim that this book is "not intended as a series of examples or stand-alone studies." This is worth looking at as a stand-alone study because this parasite is so harmful and receiving so much attention, both from scientists and population managers, and it represents a good example of the kinds of collaborative efforts discussed in Chap. 12. Protecting the critically endangered Mangrove Finch (*Camarhynchus heliobates*) from parasitism by the Philornis fly has led to the first and only captive breeding program for Galapagos birds.

1.3.5 Part V: Challenges for Management

I think it is safe to say that most studies of disease ecology in a place like Galapagos are conceived with the notion that they may be informative to management efforts on the islands, even if they are not planned with that application as the primary motivation. In fact, the Galapagos National Park requires preliminary reports of activities under seasonal research permits before leaving the islands, and the Park encourages management recommendations as part of these reports. As is explained in the final section on Challenges for Management, there are several levels of management interest in the findings of disease ecology.

In Chap. 10, Padilla, Gottdenker, Deem, and Cruz explain the government and Non-Government Organizations that interact to provide management oversight to wildlife populations in the Galapagos Islands. There are many agencies and organizations, and some of them report to others on the list. One challenging aspect of the complex network of agencies is that they change, both in structure (agencies come and go) and they change even faster in personnel. They will also explain the challenge posed by the fact that four of the 13 major islands are inhabited by humans and the remainder are not. The human inhabitants on those four islands have pet dogs and cats, and those four islands also have agricultural zones where domestic livestock are kept, including cattle, pigs, chickens, and other farmyard animals used for meat, eggs, and dairy products. There are regulations governing these activities, and it is sometimes not clear that those regulations considered wild animal health and the possibility of disease transfer from domestic to wild animals, but were perhaps more focused on human health. Recent changes in Galapagos agencies are more integrative across human-domestic animal-wild animal health.

The next set of challenges concerns those associated with quantifying the patterns that we observe with respect to where pathogens are detected, on which islands, within which species, and how we estimate the commonness of pathogens. Of course, these estimates are challenged by the fact that a highly virulent pathogen may go undetected precisely because it quickly kills the hosts who become infected, before we have an opportunity to capture and test them. Or even if it does not kill them immediately, if they “lay low” because of sickness (‘morbidity’ in epidemiological terms), we may not detect them and will underestimate the true prevalence of the pathogen (proportion of individuals in the population that are infected), or, in the worst case, may not realize it is there. In Chap. 11, Huyvaert tackles these problems and suggests some solutions, although some of the quantitative issues are tough to solve. Huyvaert proposes some modeling approaches that may help, and will certainly raise awareness to the quantitative issues.

Finally, Chap. 12 takes on the challenges of collaboration and the politics of conservation. Parker, Miller, and Goodman describe the “rules of engagement” for successful collaborations involving people from multiple institutions in multiple countries, speaking multiple languages. Successful collaborations, especially those that hope to result in conservation impact, must be based on mutual need, mutual respect, and recognition of each other’s differences, and must involve local participants as key stakeholders for long-term stability. Even with the best of intentions, collaborations sometimes fail to achieve all of their desired objectives because of factors outside of their control (such as restructuring or turnover of key government agencies). We discuss best practices and elaborate on the shortcomings and successes of two different international collaborations aimed at understanding animal health issues in the Galapagos Islands. The participants in this volume have all participated in one or both of these large collaborative efforts, and will continue to work toward the goals of securing the future of wildlife health in Galapagos.

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Part I
Colonization of Islands by Hosts and Parasites

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 km^2 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.

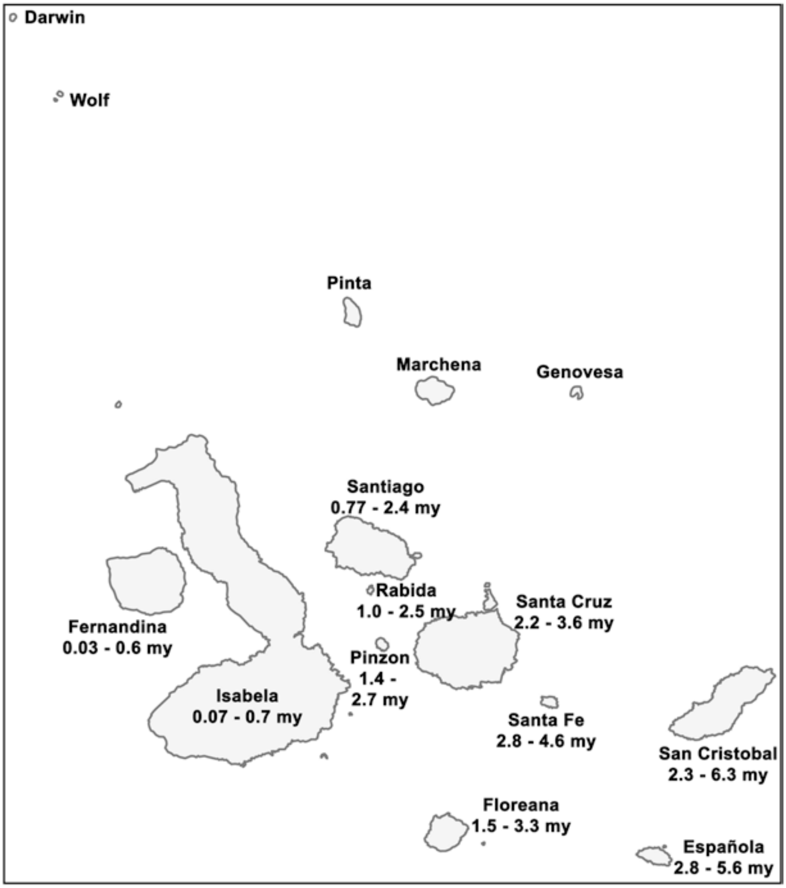

Fig. 2.1 Ages of central Galapagos Islands proposed by Geist (1996). Ages are given in million years (my) below island names. Map of the Galapagos Archipelago with main islands was modified from NordNordWest (https://commons.wikimedia.org/wiki/User:NordNordWest) under the terms of the GNU Free Documentation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

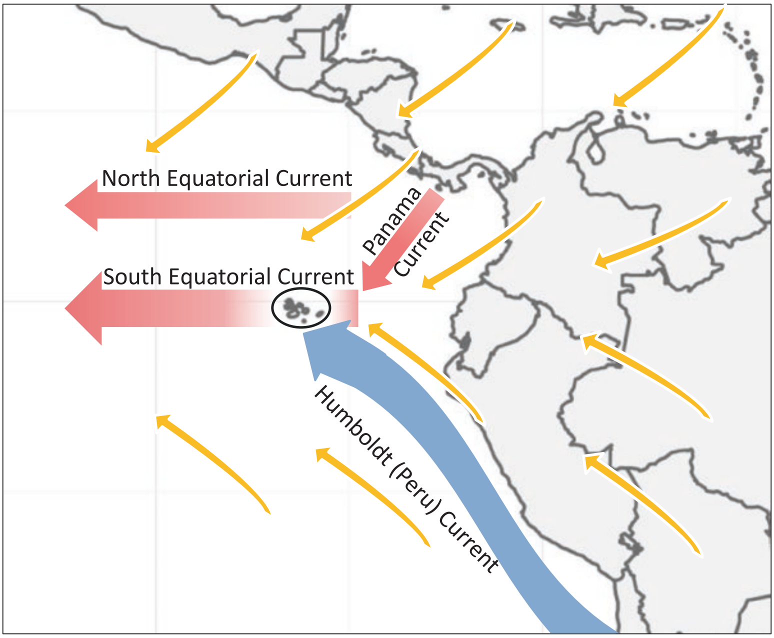

Fig. 2.2 Humboldt, Equatorial, and Panama ocean currents are responsible for the climate in Galapagos. Trade winds (represented by *yellow thin arrows*) blow southeasterly in the Southern hemisphere and northeasterly in Northern hemisphere. Galapagos Archipelago is within the *circle*

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

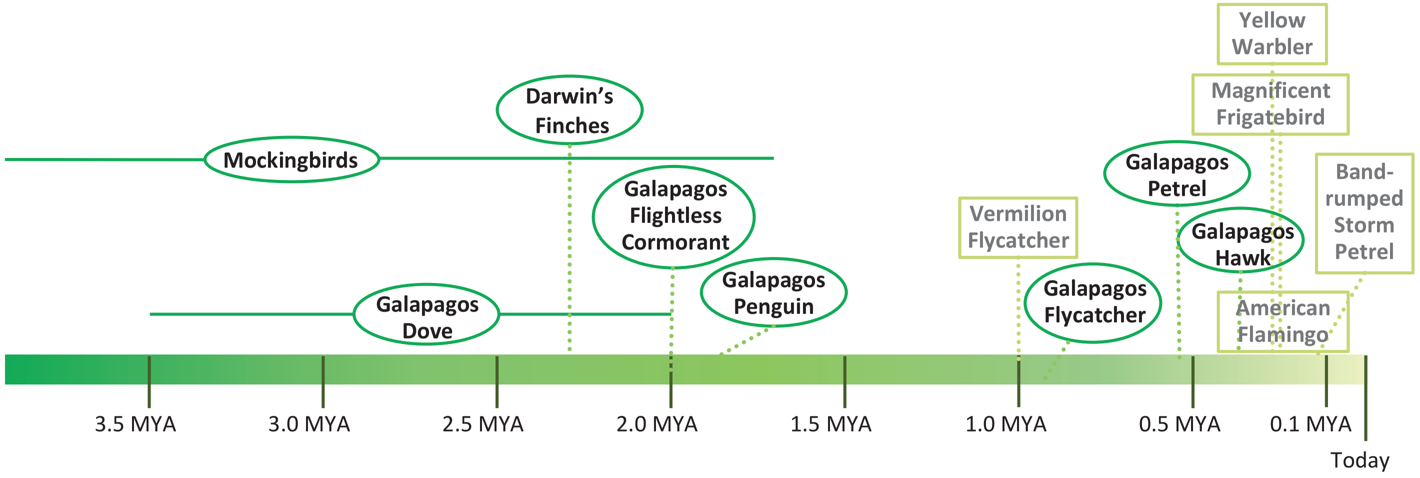

Fig. 2.3 Colonization timeline for Galapagos native birds. Maximum and minimum estimates for colonization are indicated by *horizontal bars*. MYA is million years ago. Endemic species are inside *green circles*, non-endemic species are in *yellow rectangles*. Colonization times were extracted from publications 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
Oceanodroma castro 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)
Fregata magnificens magnificens Galapagos Magnificent Frigatebird	247,000	Unknown	Unknown	Not tested	Hailer et al. (2011)
Setophaga petechia aureola Yellow Warbler	268,000	Central America	*Setophaga petechia erithachorides*/*S. p.xanthotera*	Some islands are genetically differentiated	Chaves et al. (2012)
Buteo galapagoensis Galapagos Hawk	126,000–340,000	North America	*Buteo swainsoni* (Swainson's Hawk)	All islands are differentiated	Bollmer et al. (2005, 2006), Amaral et al. (2009) and Koop et al. (2014)
Phoenicopterus ruber American Flamingo	70,000–350,000	Caribbean/South America	Conspecific Caribbean populations	Not tested	Frias-Soler et al. (2014)
Pterodroma phaeopygia Galapagos Petrel	550,000	Tropical Pacific	*Pterodroma sandwichensis* (Hawaiian Petrel)	Some islands are genetically differentiated	Friesen et al. (2006) and Welch et al. (2011)
Myiarchus magnirostris Galápagos Flycatcher	850,000	Central America	*Myiarchus tyrannulus* (Brown-crested Flycatcher)	Some islands are genetically differentiated	Sari and Parker (2012)
Pyrocephalus rubinus Vermilion Flycatcher	1,000,000	South America	All other *Pyrocephulus rubinus* subspecies	Three lineages: *P.r. dubius*, and 2 lineages within *P.r. nanus*	Carmi et al. (2016)
Spheniscus mendiculus Galapagos Penguin	1,900,000	Peru	*Spheniscus humboldti* (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
Phalacrocorax harrisi Galápagos Flightless Cormorant	2,000,000	Americas	*Phalacrocorax auritus* (Double-crested Cormorant)/*P. brasilianus* (Neotropic Cormorant)	All populations and islands are differentiated	Duffie et al. (2009) and Kennedy et al. (2009)
Zenaida galapagoensis Galapagos Dove	2,000,000–3,510,000	Unknown	*Zenaida auriculata* (Eared Dove) and *Z. graysoni* (Socorro Dove)/*Z. macroura* (Mourning Dove)	Panmixia	Johnson and Clayton (2000), Santiago-Alarcon et al. (2006) and Valente et al. (2015)
Certhidea spp., *Cactospiza* spp., *Geospiza* spp., *Camarhynchus* spp., *Platyspiza crassirostris* Darwin finches (14 species)	2,300,000	Caribbean	*Tiaris fuliginosus* (Sooty Grassquit)/ *T. obscurus* (Dull-colored Grassquit)	Panmixia for *Camarhynchus* spp. and *Geospiza fuliginosa*. 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)
Mimus spp. Galapagos mockingbirds (4 species)	1,600,000–5,500,000	Caribbean	*Mimus gundlachii* (Bahama Mockingbird)	All islands are differentiated for *Mimus parvulus*	Arbogast et al. (2006), Hoeck et al. (2010) and Lovette et al. (2012)
Information from studies not focusing on colonization of Galapagos taxa					
Sula granti Nazca Booby	<1,100,000	Unknown	*Sula dactylatra* (Masked Booby)	Some islands are genetically differentiated	Friesen et al. (2002), Patterson et al. (2011) and Levin and Parker (2012)
Sula nebouxii excisa 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
Sula sula websteri Red-footed Booby	Unknown	Unknown	Conspecific Pacific populations	Not tested	Steeves et al. (2003) and Morris-Pocock et al. (2010)
Oceanodroma tethys tethys Galapagos Storm Petrel	Unknown	Mexico	*Halocyptena microsoma* (Least Storm Petrel)	Not tested	Nunn and Stanley (1998) and Kennedy and Page (2002)
Puffinus subalaris Galapagos Shearwater	Unknown	Central Pacific	*Puffinus nativitatis* (Christmas Shearwater)	Not tested	Austin et al. (2004)
Leucophaeus fuliginosus Lava Gull	Unknown	North/Central America	*Leucopheus pipixcan* (Franklin's Gull)	Not tested	Pons et al. (2005)
Creagrus furcatus Swallow-tailed Gull	Unknown	Unknown	Basal to all other gull species (Laridae)	Not tested	Pons et al. (2005)
Anous stolidus galapagensis Brown Noddy	<1,000,000	Unknown	Unknown	Not tested	Cibois et al. (2016)
Phoebastria irrorata Waved Albatross	Unknown	Unknown	Basal to all other *Phoebastria* 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
Oceanites gracilis galapagoensis	Elliot's Storm Petrel	Procellariiformes	Hydrobatidae	Endemic	NE
Phaethon aethereus	Red-billed Tropicbird	Phaethontiformes	Phaethontidae	Indigenous	LC
Ardea alba	Great Egret	Pelecaniformes	Ardeidae	Indigenous	LC
Ardea herodias cognata	Great Blue Heron	Pelecaniformes	Ardeidae	Endemic	NE
Butorides striata sundevalli	Striated Heron	Pelecaniformes	Ardeidae	Endemic	NE
Nyctanassa violacea pauper	Yellow-crowned Night Heron	Pelecaniformes	Ardeidae	Endemic	NE
Pelecanus occidentalis urinator	Brown Pelican	Pelecaniformes	Pelecanidae	Endemic	NE
Fregata minor	Great Frigatebird	Suliformes	Fregatidae	Indigenous	LC
Anas bahamensis galapagensis	White-cheeked Pintail	Anseriformes	Anatidae	Endemic	NE
Gallinula galeata	Common Gallinule	Gruiformes	Rallidae	Indigenous	LC
Laterallus spilonota	Galapagos Rail	Gruiformes	Rallidae	Endemic	VU
Neocrex erythrops	Paint-billed Crake	Gruiformes	Rallidae	Indigenous	LC
Haematopus palliatus galapagensis	American Oystercatcher	Charadriiformes	Haematopodidae	Endemic	NE
Himantopus mexicanus	Black-necked Stilt	Charadriiformes	Recurvirostridae	Indigenous	LC
Onychoprion fuscatus crissalis	Sooty Tern	Charadriiformes	Sternidae	Indigenous	LC
Coccyzus melacoryphus	Dark-billed Cuckoo	Cuculiformes	Cucculidae	Indigenous	LC
Asio flammeus galapagoensis	Short-eared Owl	Strigiformes	Strigidae	Endemic	NE
Tyto alba punctatissima	Barn Owl	Strigiformes	Tytonidae	Endemic	NE
Progne modesta	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 wollebaeki*) 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.

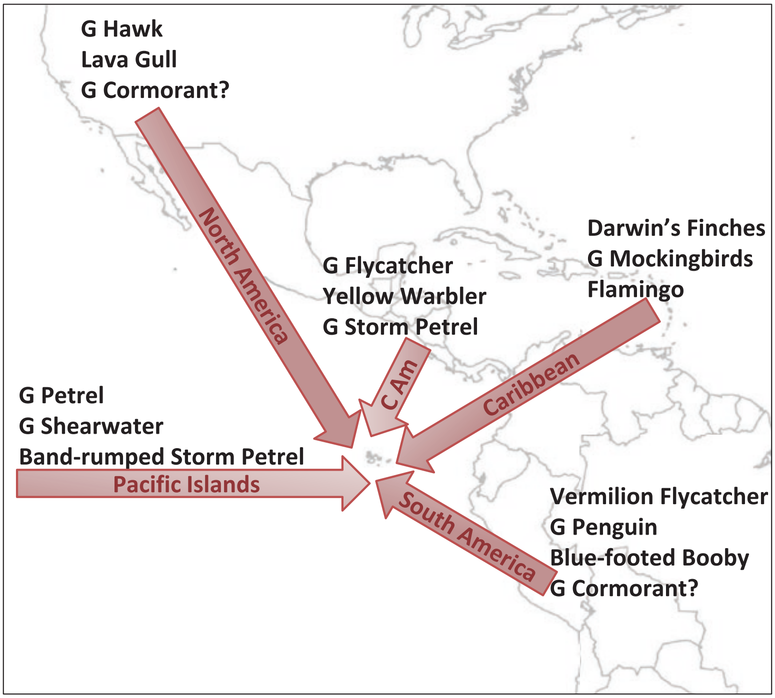

Fig. 2.4 Colonization origins of Galapagos native birds. G is Galapagos; C Am is Central America; question mark after Cormorant refers to different possible origins for this species. Species names are in Table 2.1

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 Neartic 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 Fst 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 (Floreana, 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 Floreana 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 Φst 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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Chapter 3
Colonization of Parasites and Vectors

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Abstract Colonization comprises the physical arrival of a species in a new area, but also its successful establishment within the local community. Oceanic islands, like the Hawaiian and the Galapagos archipelagos, represent excellent systems to study the mechanisms of colonization because of their historical isolation. In this chapter, we first review some of the major mechanisms by which parasites and vectors could arrive to an oceanic island, both naturally or due to human activities, and the factors that may influence their successful establishment in the insular host community. We then explore examples of natural and anthropogenic colonization of the Galapagos Islands by parasites and vectors, focusing on one or more case studies that best represent the diversity of colonization mechanisms that has shaped parasite distribution in the archipelago. Finally, we discuss future directions for research on parasite and vector colonization in Galapagos Islands.

Keywords Dispersal • Spread • Introduction • Coevolution • |Host specificity • Endemism

3.1 General Introduction

Colonization, in its biological sense, can be defined as the process by which species spread to new areas. It implies not only the physical arrival of the species, but also its successful establishment within the local community. Oceanic islands, like the

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Hawaiian and the Galapagos archipelagos, represent excellent systems to study the mechanisms of colonization because of their historical isolation. Ecosystem isolation was one of the most important premises used by MacArthur and Wilson (1967) for postulating the theory of Island Biogeography. In this landmark theory, they proposed that the number of species present in an isolated natural community is determined by both immigration and extinction rates. Immigration rates depend on the distance separating the island from potential sources of colonization (distance effect), while the size of the island limits resource and habitat availability and influences species extinction rates (species-area effect).

The theory of Island Biogeography has also been applied to the colonization of hosts by parasites (Poulin 2004; Reperant 2009). In this case, host mobility or density are considered distance effects influencing parasite immigration rate, and host body size and life-span represent species-area effects on extinction rate. However, the observed patterns of parasite species richness do not always fit these simple general laws of biogeography due to the complexity of host-parasite interactions and co-evolution (Poulin 2004; Strona and Fattorini 2014).

It is important to note that the term colonization usually refers to natural establishment. Humans have deeply changed the distribution of species and their environment, and human-aided spread of species to new areas is typically called invasion or introduction. Although this chapter is entitled colonization, it explores both natural and anthropogenic colonization of the Galapagos archipelago by parasites and disease vectors. Throughout this chapter, a broad definition of parasite will be used to include viruses, bacteria, protozoans, fungi, as well as more traditionally defined parasites such as arthropods or helminths.

In this chapter, we first review some of the major mechanisms by which parasites and vectors could arrive to an oceanic island, both naturally or due to human activities (see Table 3.1), and the factors that may influence their successful establishment in the insular host community. This introduction is not intended as an extensive review of species colonization, but rather as a way to place our understanding of parasite and vector colonization in Galapagos in a global context. In the following sections of the chapter, we then explore examples of natural and anthropogenic colonization of the Galapagos Islands by parasites and vectors, focusing on one or more case studies that best represent the diversity of colonization mechanisms that has shaped parasite distribution in the archipelago.

3.2 Parasite Arrival and Establishment in Islands: Overview of General Mechanisms

3.2.1 Natural Immigration

3.2.1.1 Direct Dispersal of Parasites

Some parasites may cover large distances without the help of a host or vector. Such direct immigration can be the result of active dispersal, and this mechanism is typically restricted to larger arthropod parasites or parasitoids with strong flying

Table 3.1 List of possible arrival modes of parasites and disease vectors in islands with examples and references cited in the text

Mode of arrival	Examples presented	References
Natural immigration		
Active direct dispersal	Parasitic wasp in Tasmania	Iqbal and Austin (2002)
	Parasitic wasp in Fiji	Masner and Johnson (2007)
Passive direct dispersal		
a. Aerial dispersal	Sugarcane rust, coffee leaf rust	Brown and Hovmoller (2002)
	Food and mouth disease virus	Keeling et al. (2001)
	Avian influenza virus	Ypma et al. (2013)
b. Water dispersal	*Vibrio cholera*	Hall-Stoodley and Stoodley (2005)
	Toxoplasma gondii	Conrad et al. (2005) and Lindsay and Dubey (2009)
Immigration with hosts		
a. Colonizing hosts	Plasmodium in lesser Antilles birds	Fallon et al. (2005)
	Hepatozoon sp. in New Zealand and Seychelles	Godfrey et al. (2011) and Harris et al. (2011)
b. Host switch after colonization	Helminth of Hawaii stream fishes	Font (2003)
c. Seabird breeding colonies	Seabirds of Iles Eparse	McCoy et al. (2016)
d. Migrating birds	Global spread of avian flu	Kilpatrick et al. (2006a, b), Olsen et al. (2006)
	Global spread of Lyme disease	Olsen et al. (1995)
Immigration with vector		
a. Wind dispersal of vectors	Japanese encephalitis virus	Ritchie and Rochester (2001)
	Bluetongue virus in Europe	Carpenter et al. (2009)
b. Vectors on host	Ticks on seabirds	Dietrich et al. (2011)
Anthropogenic introduction		
Infected invasive animals	Rats and trypanosoma in Christmas Island	Wyatt et al. (2008)
Infected domestic animals	Pigeon and Trichomonas in Mauritius	Bunbury et al. (2008)
	Avian plasmodium and avian pox in Hawaii	Warner (1968), van Riper et al. (1986), van Riper et al. (2002)
Game animal		Diamond and Veitch (1981)
Introduction of vector		
a. By commercial air transport	Culicid species in Pacific Islands	Lounibos (2002)
b. By commercial ship	Culicid species in Pacific Islands	Lounibos (2002)
Pathogen as a biocontrol agent	Myxoma virus in Australia	Fenner et al. (1957)

capacity such as parasitic wasps (Iqbal and Austin 2002; Masner and Johnson 2007). Other parasitic microorganisms have motile, free-living stages, but the distances they can travel are measured in centimeters rather than kilometers, and these short dispersals generally involve host-seeking behaviors. For instance, skin-penetrating nematodes such as hookworms can move quickly in the soil as they search for hosts using chemical cues (Castelletto et al. 2014), and uniflagellated zoospores of the highly lethal *Batrachochytrium dendrobatidis*—a widespread amphibian pathogenic fungus—can only swim for 24 h over few centimeters in still medium (Piotrowski et al. 2004). Thus, we do not consider host-seeking movements as active dispersal, at least not at a scale relevant to colonization of remote islands.

Parasites with limited or no active dispersal can still directly travel long distances under favorable environmental conditions. The aerial dispersal of plant pathogens, especially fungal spores, has largely contributed to the global spread of important crop diseases like the sugarcane rust or coffee leaf rust (Brown and Hovmoller 2002). Some animal pathogens can also survive several days or weeks outside of their host and can be spread by aerosols and reach naive hosts. Notably, wind dispersal has played a role in various outbreaks of foot and mouth disease virus and avian influenza virus in Europe (Keeling et al. 2001; Ypma et al. 2013). Other parasites may use water currents to reach new areas. Pathogenic bacterial species such as *Vibrio cholera* can form biofilms in marine and freshwater environments, facilitating their persistence and dispersal (Hall-Stoodley and Stoodley 2005). The protozoan *Toxoplasma gondii* can survive in seawater for up to 24 months and remain infective, and oocysts shed with felid feces in freshwater runoff are a likely source of infections in marine ecosystems (Conrad et al. 2005; Lindsay and Dubey 2009).

3.2.1.2 Immigration with Hosts

Long-distance travel of infected hosts is probably the most frequent natural mode of parasite immigration to islands. Ancestors of endemic species may have brought their parasites with them, leading to their coevolution in isolation. Such patterns can be found in some malaria parasite lineages restricted to endemic avian hosts in the Lesser Antilles (Fallon et al. 2005), or in *Hepatozoon* parasites of endemic reptiles in Seychelles or New Zealand (Godfrey et al. 2011; Harris et al. 2011). Newly arrived parasites can also switch to local hosts, sometimes even distantly related to their original host. This is the case for native helminth parasites of Hawaiian stream fishes that most likely colonized the islands with native fish-eating birds and marine fishes (Font 2003).

Many seabird species form large breeding colonies on islands for several months each year. The breeding grounds and foraging areas of multiple species can overlap, favoring parasite exchange (McCoy et al. 2016). Although seabirds often show high breeding site fidelity, colonies can be visited by transient birds (e.g., immature birds, failed breeders) or by infested birds deserting their colonies, which facilitates the colonization of new locations by parasites (Brown and Brown 2004; Dietrich et al. 2011). Many bird species also naturally travel long distances and may use islands as stop-over sites during their migration or foraging, carrying along parasites. Wild migrating birds and seabirds play an important role in the global spread of avian influenza and Lyme disease, respectively (Olsen et al. 1995; Olsen et al. 2006; Kilpatrick et al. 2006a).

3.2.1.3 Immigration with Arthropod Vector

Some disease vectors such as mosquitoes or midges are also capable of traveling long distances, usually with the help of aerial currents, and may bring parasites with them to new areas. For example, wind dispersal of infected midges is thought to have played a role in the spread of bluetongue virus in the Mediterranean basin and Northern Europe, and wind dispersal of infected mosquitoes is implicated in the spread of Japanese encephalitis virus to Australia (Kay and Farrow 2000; Ritchie and Rochester 2001; Carpenter et al. 2009). Infected vectors can also travel on their hosts, such as ticks (Dietrich et al. 2011) and Hippoboscid flies found on seabirds, but in such cases it is hard to determine the relative importance of the host or the vector in parasite colonization.

3.2.2 Anthropogenic Introduction

Human activities have a continuously increasing impact on the environment in direct relation with their unique capacity to innovate and harvest natural resources. Human colonization has been followed by species extirpation since prehistoric times (Milberg and Tyrberg 1993). The introduction of invasive species and diseases by humans is a major cause of disturbance of natural communities around the globe, and islands have not been spared (Blackburn et al. 2004; Bellard et al. 2016). Parasite invasions of islands can originate from accidental transport of invasive hosts and vectors (Wyatt et al. 2008), or the deliberate introduction of domestic animals (Bunbury et al. 2008) and game (Diamond and Veitch 1981). Probably one of the most famous examples of the impact of introduced parasites on insular wildlife is the decline of the Hawaiian endemic avifauna following the introduction of the avian malaria *Plasmodium relictum,* avianpox virus, and their mosquito vector *Culex quinquefasciatus* (Warner 1968; van Riper et al. 1986, 2002). In some rare cases, parasites are deliberately introduced in new areas as a mean to control invasive species. The most notorious example is the introduction of myxoma virus in Australia in the 1950s to control invasive rabbit populations (Fenner et al. 1957).

The globalization of human activities in the last decades has multiplied the risks of parasite emergence to an unprecedented scale (Daszak et al. 2000; Jones et al. 2008). The ever-expanding air transport network has dramatically increased the risk of global epidemics by facilitating the movement of infected hosts and disease vectors (Mangili and Gendreau 2005; Tatem et al. 2006a, b). Commercial ships have also contributed to the spread of many invasive species, including parasites and disease vectors across the globe (Ruiz et al. 2000; Lounibos 2002).

Habitat destruction and intensification of agriculture have also led to human encroachment into wildlife habitat and loss of biodiversity, increasing the risk of pathogen spill-over between humans, domestic animals, and wildlife (Daszak et al. 2001; Keesing et al. 2010). Due to their isolation and high level of endemism, species on oceanic islands are especially at risk in the face of these modern challenges (Kier et al. 2009; Bellard et al. 2016). Again we can refer to the example of Hawaii, where human activities have permitted secondary introduction of different strains of *Culex quinquefasciatus* in the archipelago, which has been associated with an increase in the altitudinal range of the mosquito and in malaria virulence, further increasing the impact of the disease on the endemic fauna (Fonseca et al. 2000, 2006).

3.2.3 Establishment After Arrival

The ecological processes associated with island colonization by hosts and parasites, such as the island syndrome and host switching, will be the subjects of Chaps. 4–7. Here, we will briefly mention some key factors influencing the success of parasite establishment in island communities.

Parasite colonization fundamentally depends on host colonization success (see Chap. 2), and on availability of suitable native hosts. During host colonization, the probability of parasite establishment and co-evolution with their host will also depend on parasite transmission efficiency. Parasites will have a higher risk of extinction when founding host populations are small, when stochastic events result in host extinction, and sometimes, when the host population front moves faster than the disease transmission front (Bar-David et al. 2006; MacLeod et al. 2010).

Parasite colonization will also depend on introduction effort, also called propagule pressure (Lockwood et al. 2005). Parasite establishment is more likely in situations where there are larger numbers of individual parasites arriving to the new area and more numerous arrival events. For parasites, introduction effort can be measured at the level of host individuals, populations, or species (Poulin 2004). Notably, parasites in aggregated distributions among few hosts are more susceptible to “missing the boat” and going extinct (Paterson et al. 1999; MacLeod et al. 2010). If its host fails to establish, parasites go extinct with them, unless other suitable hosts are present. Large and dense breeding colonies of seabirds are good host candidates for parasites because they provide a large number of potential hosts and regular opportunities of transmission (McCoy et al. 2016).

In comparison to continental species, endemic insular species may have a lower diversity of evolved immune defenses, probably as a consequence of their reduced parasite assemblages, which can increase their susceptibility to arriving parasites (Frankham 1997; Matson 2006). Infecting naive hosts allows parasites to remain in the new ecosystem even if the original, colonizing host goes extinct or is only transient (Smith and Carpenter 2006). Therefore, the capacity of the parasite to infect a wide range of hosts contributes greatly to its persistence after colonization. It has been argued that all parasites, except true specialists, can switch hosts rapidly if they can exploit newly available resources without having to evolve novel capacities (Hoberg and Brooks 2008). Lower prevalence and smaller distributions of host-specific avian blood parasites in island systems compared to widespread host-generalists provide support for this idea (Beadell et al. 2004; Ewen et al. 2012; Clark and Clegg 2015).

For vector-borne parasites, parasite establishment will also depend on the presence of a suitable vector. Parasites with high vector specificity have more restricted ranges than parasites with a wide range of vectors (Ishtiaq et al. 2010). Other important factors are vector habitat preferences, host specificity, and dispersal capacity (Ishtiaq et al. 2010). For this reason, the study of insular vector populations is critical to understand vector-borne parasite colonization.

3.3 Natural Parasite Colonization in the Galapagos Archipelago

Based on data compilations by Deem et al. (2011), Parker et al. (2006), and Sari et al. (2013), a total of 147 species of parasites and disease vectors have been identified in the Galapagos archipelago (see Table 3.2, Fig. 3.1). Of those, 95 could have arrived naturally, based on taxonomic or phylogenetic data, and their distribution in the native fauna. Most of these natural colonizations are directly transmitted parasites or arthropod disease vectors, although a relatively large number of native vector-borne blood parasites have been identified (see Fig. 3.1). These numbers are unlikely to accurately reflect the absolute or relative abundance of native and introduced parasites, as some host-parasite systems have been more heavily studied than others (e.g., parasites of the Galapagos avian fauna).

3.3.1 Colonization with a Vertebrate Host

In Galapagos, there are several examples of parasites that have naturally colonized the islands with their hosts (see Table 3.2). These are obligate parasites that are commonly found in close association with their bird hosts, usually with high prevalence and high densities on any given host. This happens because when hosts colonize a new area, less common parasites may have a higher chance of "missing the boat" (Paterson et al. 1999). Feather mites (Acari: Astigmata), lice (Insecta: Phthiraptera), and blood parasites (Apicomplexa: Haemosporida) represent good examples of colonizers that arrived to Galapagos with their vertebrate host. In order to make inferences about parasite arrival, we need to study the parasites from Galapagos animals and from their closest related continental species, which requires an understanding of the colonization history of the hosts themselves (see Chap. 2).

Table 3.2 Parasites recorded in the Galapagos Islands and their likely mode of arrival

Species	Type	Known host in Galapagos	Likely mode of arrival
Natural colonization			
Vector-borne parasites			
Myialges caulotoon	Mite	Galapagos hawk, flightless cormorant	Colonizing or migrating birds
Und. *Haemoproteus* spp. (8)[a]	Protozoa	Swallow-tailed gull, Galapagos dove,	Colonizing or migrating birds
		Frigatebird spp., Nazca booby	
Und. Microfilaria[a]	Nematode	Flightless cormorant, Galapagos penguin	Colonizing or migrating birds
Und. *Parahaemoproteus*	Protozoa	Blue-footed booby	Colonizing or migrating birds
Und. *Plasmodium* spp. (3)	Protozoa	Galapagos penguin	Migrating birds
Und. *Trypanosoma* sp.[a]	Protozoa	Galapagos hawk	Colonizing birds
Directly-transmitted parasites and mites			
Amerodectes atyeoi	Mite	Darwin's finches	Colonizing birds
Analges spp. (4)	Mite	Galapagos mockingbird spp.	Colonizing birds
Antartophtirus microchir	Louse	Galapagos sea lion	Colonizing or migrating mammals
Austrogoniodes demersus	Louse	Galapagos penguin	Colonizing or migrating birds
Atractis marquezi[a]	Nematode	Galapagos tortoise	Colonizing reptiles
Brueelia spp. (3)	Louse	Most passerines	Colonizing or migrating birds
Chlamydophila psittaci	Bacteria	Galapagos penguin, flightless cormorant, Galapagos dove	Colonizing or migrating birds
Colpocephalum spp. (3)	Louse	Galapagos hawk, Magnificent and Great frigate birds	Colonizing or migrating birds
Columbicola macrourae	Louse	Galapagos dove, Galapagos hawk	Colonizing or migrating birds
Contracecum sp.	Nematode	Brown pelican	Colonizing or migrating birds
Craspedorrhynchus sp.[a]	Louse	Galapagos hawk	Colonizing birds
Degeeriella regalis	Louse	Galapagos hawk	Colonizing birds
Dermanyssus sp.	Mite	Small ground finch	Colonizing birds
Dermoglyphus sp.	Mite	Darwin's finches	Colonizing birds
Eidmanniella albescens	Louse	Boobies	Colonizing or migrating birds
Fregatiella aurifasciata	Louse	Magnificent and great frigatebirds	Colonizing or migrating birds

(continued)

Table 3.2 (continued)

Species	Type	Known host in Galapagos	Likely mode of arrival
Eimeria spp. (2)	Protozoa	Galapagos reptiles	Colonizing reptiles
Eimeria palumbi[a]	Protozoa	Galapagos dove	Colonizing birds
Isospora spp. (6)[a]	Protozoa	Darwin's finches.	Colonizing birds
Isospora insularius[a]	Protozoa	Galapagos reptiles	Colonizing reptiles
Mesalgoides geospizae	Mite	Darwin's finches	Colonizing birds
Menacanthus distinctus[a]	Louse	Galapagos flycatcher	Colonizing birds
Myrsidea spp. (3)	Louse	Darwin's finches, Galapagos mockingbirds.	Colonizing birds
		Yellow warbler	
Nycteridocaulus sp.[a]	Mite	Galapagos flycatcher	Colonizing birds
Orthohalarachne diminuata	Mite	Galapagos sea lion	Colonizing or migrating mammals
Pectinopygus spp. (6)	Louse	Flightless cormorant, boobies, Frigatebirds	Colonizing or migrating birds
Philophthalmus zalophi[a]	Trematode	Galapagos sea lion	Colonizing or migrating mammals
Philopterus insulicola	Louse	Galapagos vermillon flycatcher	Colonizing birds
Physconelloides galapagensis[a]	Louse	Galapagos dove, Galapagos hawk	Colonizing or migrating birds
Piagetiella sp.	Louse	Brown pelican	Colonizing or migrating birds
Polysporella genovesae[a]	Protozoa	Galapagos mockingbirds	Colonizing birds
Natural colonization (continued)			
Directly-transmitted parasites and mites (continued)			
Proctophyllodes darwinii[a]	Mite	Darwin's finches	Colonizing or migrating birds
Renicola sp.	Trematode	Brown pelican	Colonizing or migrating birds
Ricinus marginatus[a]	Louse	Galapagos flycatcher	Colonizing birds
Strelkoviacarus spp.[a]	Mite	Darwin's finches	Colonizing or migrating birds
Trouessartia spp. (2)[a]	Mite	Small ground finch, Galapagos flycatcher	Colonizing birds
Tyrannidectes berlai[a]	Mite	Galapagos flycatcher	Colonizing birds
Xolalges palmai	Mite	Darwin's finches	Colonizing or migrating birds
Zonorchis meyeri[a]	Trematode	Galapagos rail	Colonizing birds
Disease vectors			
Aedes taeniorhynchus[a]	Fly	Multiple reptiles, mammal, and avian species	Direct colonization

(continued)

Table 3.2 (continued)

Species	Type	Known host in Galapagos	Likely mode of arrival
Amblyomma spp. (2[a] + 3)	Tick	Marine iguana, Galapagos tortoise, land iguana	Colonizing reptiles
Icosta spp. (2)	Fly	Galapagos hawk, flightless cormorant	Colonizing or migrating birds
Microlynchia galapagoensis[a]	Fly	Galapagos dove, mockingbrid spp.	Colonizing birds
Olfersia spp. (3)	Fly	Frigatebirds, flightless cormorant	Colonizing or migrating birds
Ornithodoros spp. (2[a] + 1)	Tick	Marine iguana, Galapagos tortoise, land iguana	Colonizing reptiles
Ornithoica vicina	Fly	Unknown	Colonizing or migrating birds
Tabanus vittiger[a]	Fly	Multiple reptiles, mammal, and avian species	Direct colonization
Vatacarus spp. (3)	Tick	Marine iguana, waved albatross	Colonizing reptiles and birds
Anthropogenic colonization			
Vector-borne parasites			
Avipoxvirus (canarypox)	Virus	Galapagos finches, Galapagos mockingbird, Yellow warbler	Introduced or migrating birds
Avipoxvirus (fowlpox)	Virus	Chicken	Introduced chicken
Dirofilaria immitis	Nematode	Galapagos sea lion, dog	Introduced dogs
Directly-transmitted parasites			
Ancylostoma caninum	Nematode	Dog	Introduced dogs
Ascaridia galli	Nematode	Chicken	Introduced chicken
Avian *Adenovirus*	Virus	Chicken, Galapagos finches, waved albatross	Introduced chicken
Avian *Birnavirus*	Virus	Chicken	Introduced chicken
Avian *Coronavirus*	Virus	Chicken	Introduced chicken
Avian encephalomyelitis virus	Virus	Chicken	Introduced chicken
Avian P*aramyxovirus* 1	Virus	Chicken, Galapagos finches	Introduced chicken
(Newcastle virus)			
Bartonella spp.	Bacteria	Dog	Introduced dogs
Bovicola spp.	Louse	Goat, Galapagos hawk	Introduced goat
Canine *Adenovirus*	Virus	Dog	Introduced dogs
Canine *Coronavirus*	Virus	Dog	Introduced dogs

(continued)

Table 3.2 (continued)

Species	Type	Known host in Galapagos	Likely mode of arrival
Canine distemper virus	Virus	Dog	Introduced dogs
Canine parainfluenza virus	Virus	Dog	Introduced dogs
Canine *Parvovirus*	Virus	Dog	Introduced dogs
Capillaria sp.	Nematode	Chicken	Introduced chicken
Anthropogenic colonization			
Directly-transmitted parasites (continued)			
Cryptosporidium sp.	Protozoa	Dog	Introduced dogs
Davainea proglottina	Cestode	Chicken	Introduced chicken
Dispharynx sp.	Nematode	Chicken	Introduced chicken
Ehrlichia/Anaplasma spp.	Bacteria	Dog	Introduced dogs
Epidermoptes bilobatus	Mite	Chicken	Introduced chicken
Feline *Herpesvirus*	Virus	Cat	Introduced cats
Feline *Calicivirus*	Virus	Cat	Introduced cats
Gallid *Herpesvirus* (2) (Marek's disease)	Virus	Chicken	Introduced chicken
Gammacoronavirus	Virus	Chicken	Introduced chicken
Giardia sp.	Protozoa	Dog	Introduced dogs
Isospora canis	Protozoa	Dog	Introduced dogs
Leishmania donovani	Protozoa	Dog	Introduced dogs
Macrorhabdus sp.	Bacteria	Chicken	Introduced chicken
Mycoplasma gallisepticum	Bacteria	Chicken	Introduced chicken
Mycoplasma haemocanis	Bacteria	Dog	Introduced dogs
Mycoplasma haemofelis	Bacteria	Dog	Introduced dogs
Avian *Orthoreovirus*	Virus	Chicken	Introduced chicken
Oxyspirura mansoni	Nematode	Chicken	Introduced chicken
Papillomavirus bovino	Virus	Cattle	Introduced cattle
Feline panleukopenia virus	Virus	Cat	Introduced cats
Philornis downsi	Fly	Galapagos finch, flycatcher, mockingbird spp.	Human transport stowaway
Raillietina echinobothrida	Cestode	Chicken	Introduced chicken
Sarcocystis canis	Protozoa	Dog	Introduced dogs
Sarcodexia lambens	Fly	Darwin finch spp.	Human transport stowaway, Introduced birds
Tetrameres sp.	Nematode	Chicken	Introduced chicken
Toxocara canis	Nematode	Dog	Introduced dogs
Toxoplasma gondii	Protozoa	Cat, Galapagos penguin, cormorant	Introduced cats
Trichomonas gallinae	Protozoa	Rock dove, Galapagos dove	Introduced rock doves
Wolbachia pipiens	Bacteria	Dog	Introduced dogs

(continued)

Table 3.2 (continued)

Species	Type	Known host in Galapagos	Likely mode of arrival
Disease vectors			
Aedes aegypti	Fly	Human	Human transport stowaway
Culex quinquefasciatus	Fly	Mammals and birds	Human transport stowaway
Culicoides pusillus	Fly	Mammals	Human transport stowaway
Simulium punctatum	Fly	Humans	Human transport stowaway

This list is based on compilations done by Deem et al. (2011), Parker et al. (2006), and Sari et al. (2013). The type « fly » includes insects of the order Diptera, and the type « louse » regroups insects of the order Phthiraptera. “Und”, undescribed species. Numbers between brackets in front of species names indicates the number of species identified

[a]Species confirmed to be native by taxonomic or phylogenetic studies

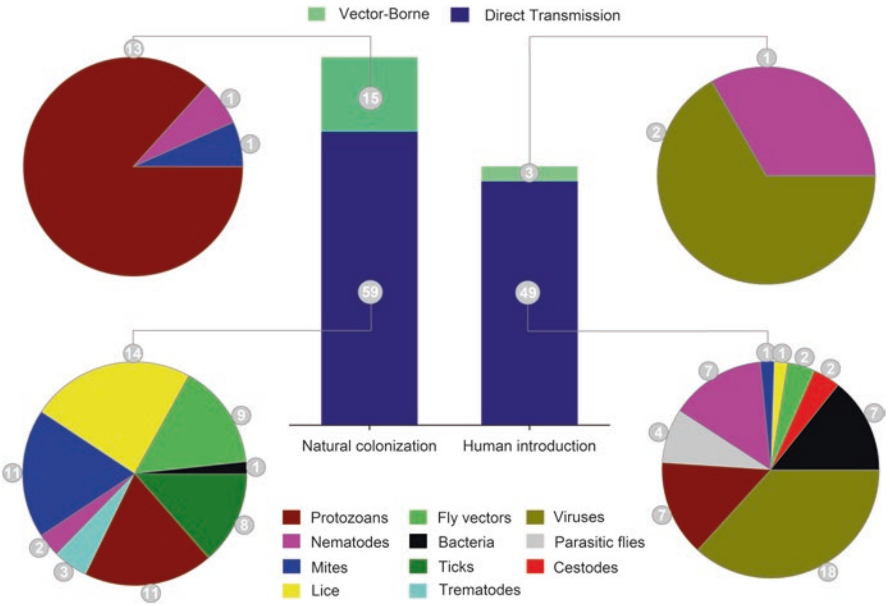

Fig. 3.1 Graphical representation of the number and different types of parasites and vectors identified in the Galapagos Islands

3.3.1.1 Co-colonization of Hosts and Parasites: Examples from Lice and Mites on the Galapagos Flycatcher and the Galapagos Hawk

The Galapagos flycatcher (*Myiarchus magnirostris*) colonized the Galapagos Islands about 850,000 years ago, and their closest relatives are the Brown-crested flycatchers (*Myiarchus tyrannulus*) from Central America (Sari and Parker 2012). In order to investigate which parasites colonized the archipelago with their hosts, Sari et al. (2013) sampled mites, lice, and blood parasites from Galapagos flycatchers on seven Galapagos islands and also from Brown-crested flycatchers at four locations in Costa Rica. These authors described a suite of six mite and louse species infecting Galapagos flycatchers, of which five species are shared with the Brown-crested flycatchers, leading to the conclusion that these mites and lice arrived to Galapagos together with their bird hosts when they naturally colonized the archipelago. Taking a closer look at the morphology of this ectoparasite assemblage, Sari et al. (2013) reported that only one of these species, a mite from the genus *Nycteridocaulus* (Family Proctophyllodidae), has evolved evident morphological differentiation between the two host species, leading to the conclusion that the *Nycteridocaulus* from the Galapagos flycatcher is probably not conspecific with that from the Brown-crested flycatcher. The other mite and louse species have the same morphological characteristics and taxonomic classification, for both host species. However, genetic distance between *Ricinus marginatus* lice collected from both host species was found to be almost ten times larger than the genetic distance between their hosts (Sari et al. 2013). Both hosts and their lice have been evolving in allopatry for about 850,000 years (see Chap. 2), but evident speciation was only observed in the bird hosts (Sari et al. 2013). These findings add to the body of knowledge indicating that morphological evolution tends to be more conservative in parasites than their hosts (Klassen 1992) and suggest that the process of speciation for lice can take much longer than it takes for their hosts, as mentioned by McDowall (2000).

A similar pattern was also observed for the Galapagos Hawk (*Buteo galapagoensis*) (Whiteman et al. 2007, 2009), a more recent arrival to Galapagos than the Galapagos flycatcher. The Galapagos hawk colonized the archipelago about 300,000 years ago and its closest related continental species is the Swainson's Hawk (*Buteo swainsoni*) (Bollmer et al. 2006; Amaral et al. 2009) (see Chap. 2). Five species of ectoparasites have been found on hawks on several of the Galapagos islands: one hippoboscid fly (*Icosta nigra*), three species of lice (*Degeeriella regalis*, *Colpocephalum turbinatum*, and *Craspedorrhynchus* sp.), and one skin mite (*Myialges caulotoon*) (Whiteman et al. 2006, 2007, 2009). All these species are also found on Swainson's hawks and are thought to have colonized Galapagos together with their hawk host (Price et al. 2003; Parker et al. 2006). Whiteman et al. (2009) looked at variation in both morphology and DNA sequences for one of these species, the head louse *Craspedorrhynchus* sp., in populations of Galapagos hawks and Swainson's hawks in North and South America. They found approximately 10% genetic divergence between lice from the two host species, while almost no genetic differentiation was found between the Galapagos and the Swainson's hawks used in this study (only one base pair in 497 nucleotides sequenced of COI). In contrast, hawks from Galapagos and Swainson's hawks are strikingly different in morphology but the *Craspedorrhynchus* lice found on the two hosts showed a lot of overlap in morphological characteristics. Subtle morphological differences, however, were observed in the head and genitalia of lice between the two host species, allowing the identification of their geographical origin and possibly lineage diversification.

Parasites that colonized the Galapagos with their vertebrate hosts share patterns of distribution and evolutionary history with their hosts. Rivera-Parra et al. (2015) showed that the species identity of the host was more important than sampling location for determining the phylogenetic relationships within each species of louse parasitizing two related seabird species, despite the fact that the hosts breed together in dense mixed-species colonies. However, these lice have different prevalence on different islands, demonstrating that the relationships among parasites, hosts, and islands are idiosyncratic (Rivera-Parra et al. 2014). Nematode parasites that colonized Galapagos together with the founding population of the Galapagos tortoises (*Chelonoidis nigra* species complex) also show a similar island-dependent distribution (Fournié et al. 2015). Each Galapagos tortoise species is found only on one island, and each island has a different combination of nematodes. Fournié et al. (2015) suggested that the observed pattern could have resulted from a neutral process of founder events following the arrival of tortoises to Galapagos.

3.3.1.2 The Potential Role of Migratory Birds in Parasite Colonization: The Arrival of *Plasmodium* (Avian Malaria) to Galapagos

Parasites might also colonize the Galapagos archipelago via migratory or vagrant birds. For example, *Plasmodium* parasites detected in Galapagos endemic passerine bird species may have arrived with migratory Bobolinks (*Dolichonyx oryzivorus*; see Fig. 3.2) (Levin et al. 2013). Four lineages of *Plasmodium* parasites have been identified in the Galapagos (Levin et al. 2009, 2013). One lineage was repeatedly detected in Galapagos penguins and occasionally in yellow warblers and the other three were only detected in one or a handful of Galapagos birds at one location, at one given time (Levin et al. 2013). A very large sampling effort (nearly 4000 birds molecularly screened for blood parasites) was needed in order to reveal these few rare lineages. Interestingly, two of the rare lineages were perfect DNA matches with *Plasmodium* lineages amplified from North American breeding bobolink samples (Levin et al. 2013). Although this is not confirmation that migratory bobolinks introduced these rare lineages to the Galapagos, it is evidence that the islands may be exposed to more potential parasite introductions than previously thought. It is not currently known whether these rare lineages have established in the islands.

Because bobolinks spend time in both the southern and northern hemispheres during mosquito breeding season, they probably acquire blood parasites in both locations. By comparing the blood parasites found in North American breeding bobolinks to those found in the brown-headed cowbird, a short-distance migrant that breeds in sympatry, the authors were able to begin teasing apart the potential origins of the rare Galapagos *Plasmodium* lineages (Levin et al. 2016). If the Galapagos *Plasmodium* lineage is shared between bobolinks and cowbirds and pre-

Fig. 3.2 Picture of Bobolink (*Dolichonyx oryzivorus*) captured in Galapagos (Photo: Jenn Megyesi)

dominantly matches DNA sequences from other North American hosts, the colonizing lineage is likely of North American origin. If this lineage is detected in bobolinks but not cowbirds and matches predominantly South American sequences, then the origin is mostly likely South American. Bobolinks stop over in Galapagos only during their southward migration, but could still harbor chronic infections by parasites acquired many months before, while overwintering. Indeed, one of the *Plasmodium* lineages found in Galapagos birds was likely of North American origin, while the other match was likely from South America (Levin et al. 2016). More work is needed to further understand the probability of colonization by blood parasites (and other parasites) via migratory birds. Recently, several bobolinks have been sampled in Galapagos in October during migration (P. Parker, personal communication). By far the most abundant migratory birds in Galapagos are shorebirds, and to our knowledge, none have been tested for blood parasites.

3.3.2 Colonization with/of Vectors

Multiple blood-feeding arthropods with the capacity to disperse and transmit parasites may have naturally colonized the Galapagos archipelago (see Table 3.2, Fig. 3.1). In all the cases, we have little knowledge of either their origin and native status, or their exact role as disease vectors in Galapagos. The origin and phylogenentic relationships of the only mosquito native to the Galapagos Islands, *Aedes taeniorhynchus,* are probably the best studied (Bataille et al. 2009a), although its role as a disease vector is still not clear. Conversely, the role of Hippoboscid flies (four genera and seven species in Galapagos; see Table 3.2 and Fig. 3.1) in the transmission of avian blood parasites has been well studied (Valkiunas et al. 2010; Levin et al. 2011, 2012), but their origin is uncertain. These two contrasting cases will be explored further below.

Two ticks of the genus *Ornithodoros* infecting reptiles are endemic to the Galapagos Islands (Wikelski 1999). Two other *Amblyomma* and three *Vatacarus* ticks parasitizing reptiles and one avian *Ornithodoros* species are also found in the archipelago and probably arrived naturally with their hosts. All these arthropods could be involved in the transmission of *Hepatozoon* parasites, mainly through ingestion by the vertebrate host (Smith 1996; Bataille et al. 2012). One horse-fly species of the genus *Tabanus* has also been classified as endemic to Galapagos (Sinclair 2017) and can feed on Galapagos reptiles (Philip 1976, 1983), but its role in disease transmission is completely unknown.

As argued in the introduction of this chapter, it is hard to determine whether a native vector, a native host, or both brought a colonizing parasite to Galapagos (see Sect. 3.1). Combined phylogenetic studies of parasite, vector, and host may help resolve this issue. This type of study has been carried out with mites vectored by hippoboscid flies and infecting endemic Galapagos birds (Whiteman et al. 2006), although this study focused on parasite population structure and host specificity rather than on their origin (see Chap. 8).

3.3.2.1 The Black Salt Marsh Mosquito (*Aedes taeniorhynchus*): A Successful Endemic Vector with Unclear Role in Galapagos Disease Ecology

Aedes taeniorhynchus is widely distributed in temperate and tropical coastal areas of the New World (Lang 2003). It breeds primarily in temporary-water habitats, producing huge broods after flood or heavy rains. The species is widely distributed across the Galapagos Islands. The presence of *A. taeniorhynchus* in the archipelago was first recorded in the late 1880s (Howard 1889). It was suggested early on that *A. taeniorhynchus* might have naturally reached the archipelago before the arrival of humans (Hardy 1960). On the other hand, pirates and later whalers frequently visited the archipelago between the sixteenth and nineteenth centuries, giving multiple opportunities to introduce *A. taeniorhynchus.*

To tackle this question, Bataille et al. (2009a) performed phylogenetic analyses using mitochondrial and nuclear DNA markers on *A. taeniorhynchus* specimens collected across the Galapagos archipelago and across the species' continental range. All analyses placed the Galapagos population of *A. taeniorhynchus* within one single coherent cluster clearly separated from the continental mosquito populations. This result suggests that the Galapagos population of *A. taeniorhynchus* originated from a single colonization event and now represents a distinct evolutionary unit divergent from the continental populations. Molecular clock analysis estimated that the Galapagos and continental clades diverged 176,000 years ago (95% confidence interval: 93,000–352,000 years). Although imprecise, this estimation demonstrated that the colonization by *A. taeniorhynchus* was not human-driven.

Some characteristics of the biology of *A. taeniorhynchus* support the hypothesis that this mosquito had the capacity to naturally colonize the Galapagos Islands and successfully establish itself across the archipelago. First, the strong flying capacity of *A. taeniorhynchus* is well known, and long-distance dispersal has been observed various times in this species (Provost 1951; Bello et al. 2005). Arrival of *A. taeniorhynchus* in Galapagos could have been facilitated by the strong wind and oceanic current found in the Intertropical Convergence Zone during cyclic climatic fluctuations such as El Niño events (Peck 1994). Second, *A. taeniorhynchus* lays desiccation-resistant eggs, which has been significantly associated with the success of invasive mosquito introductions in new areas (Juliano and Lounibos 2005). Third, larvae of *A. taeniorhynchus* successfully grow in water with a wide range of salinity (Clark et al. 2004), which gives them the possibility to breed in a wide range of habitats across the archipelago, notably in the mangroves found throughout the coasts of the archipelago.

The role of *Aedes taeniorhynchus* as a disease vector in Galapagos is still poorly understood, but is likely to be important (see Fig. 3.3). This species has a wide distribution, high population density, and strong dispersal capacity (Bataille et al. 2010, 2011) (see Chap. 8), so it represents an ideal vector for native and invasive mosquito-borne parasites. Moreover, it feeds opportunistically on a wide range of vertebrate hosts including birds, mammals, and reptiles (Bataille et al. 2012). This species could thus act as a bridge vector across most of Galapagos endemic wildlife (Kilpatrick et al. 2005).

Swarms of mosquitoes can be an important nuisance for Galapagos wildlife. For example, waved albatrosses (*Phoebastria irrorata*) on Española island were observed deserting their nests and neglecting their eggs due to mosquito harassment (Anderson and Fortner 1988). *Aedes taeniorhynchus* is a competent vector for the transmission of various viruses, including West Nile virus (Hardy et al. 1984; Turell et al. 1994, 2001), but, fortunately, none of those are currently present in the archipelago. *Aedes taeniorhynchus* is also considered an important vector of the dog heartworm (*Dirofilaria immitis*) (Labarthe et al. 1998; Labarthe and Guerrero 2005). The disease was introduced with dogs in Galapagos Islands (Levy et al. 2008), but the role of *A. taeniorhynchus* in its transmission, notably to Galapagos sea lions and fur seals (Dunn and Wolke 1976, Sato et al. 2002), has not been verified.

PCR-based parasite screening identified the presence of *Haemoproteus* parasites and of microfilarial nematodes in pools of mosquito thoraces collected in Fernandina and Isabela Islands (Bataille et al. 2012). However, these results do not provide direct evidence for the role of *A. taeniorhynchus* in the transmission of these parasites. Mosquitoes are not the typical vectors of *Haemoproteus* spp., although some studies have supported this possibility (Ishtiaq et al. 2008). Galapagos microfilarial nematodes infect the flightless cormorants and the

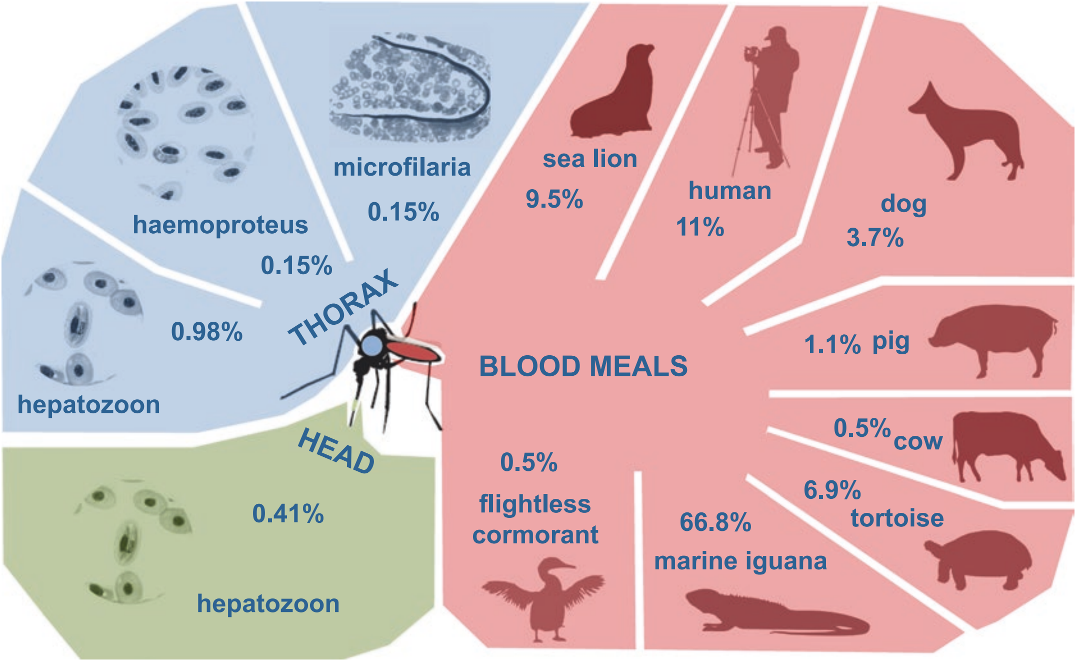

Fig. 3.3 Blood-feeding patterns and parasite infection rates in pools of thoraces and heads of the black salt marsh mosquito (*Aedes taeniorhynchus*) in Galapagos (from Bataille et al. 2012)

Galapagos penguins (Merkel et al. 2007). They may be transmitted by multiple vector species, but *Aedes taeniorhynchus* is thought to be one important vector for this parasite, because microfilariae prevalence across its hosts' ranges correlates with ecological factors suitable for *A. taeniorhynchus* populations (Siers et al. 2010), and this mosquito was shown to feed on cormorants (Bataille et al. 2012). *Hepatozoon* parasites were also detected by PCR in both thoraces and heads of mosquitoes. *Aedes taeniorhynchus* could be involved in the transmission of this parasite by accidental ingestion of infected mosquitoes, but maybe also by mosquito bites (Telford et al. 2001). This mosquito could also be a mechanical vector (i.e., transfer of the parasite without passage within the vector necessary for the parasite's life cycle) of avipoxvirus between birds in the archipelago (Thiel et al. 2005).

3.3.2.2 Hippoboscid Flies (Hippoboscidae): Vectors of Unclear Origin with an Important Role in Blood-Parasite Transmission

Hippoboscid flies are obligate, blood-feeding ectoparasites found on birds and mammals. Although some are wingless (e.g., sheep ked), most hippoboscids have fully functional wings. Despite the ability to fly, hippoboscids tend to remain closely associated with their hosts, with only one off-host life stage: female hippoboscids lay a single, late-instar larva, which pupates in the ground. Hippoboscid flies are common on Galapagos seabirds, the Galapagos hawk, and the Galapagos dove (Whiteman et al. 2007; Valkiunas et al. 2010; Levin et al. 2012) (see Fig. 3.4). The flies tend to be very host-specific, with one fly species per host species (or a few closely related host species). For example, over the course of sampling >100 flies from great and magnificent frigatebirds and blue-footed, red-footed, and Nazca boobies, the species of hippoboscid that infects boobies, *Olfersia aenescens*, was never found on a frigatebird and vice versa, despite the fact that these seabirds often breed in dense, multi-species colonies with ample opportunity for flies to host-switch (I. Levin, personal observation.). Hippoboscid flies are definitive hosts for

Fig. 3.4 Hippoboscid fly on a Nazca booby (*Sula granti*; photo: Iris I. Levin)

blood parasites in the subgenus *Haemoproteus haemoproteus* (Valkiunas 2005; Levin et al. 2011). Because of the host-specificity of the flies, lineages of *H. haemoproteus* are often specific to a particular host and fly pair (Valkiunas et al. 2010; Levin et al. 2011, 2012).

For reasons already mentioned, it is difficult to determine the order and combination of arrival in Galapagos: did colonizing birds arrive infected with flies and *Haemoproteus*? Or did the flies and *Haemoproteus* arrive later? Perhaps the most parsimonious explanation is that colonizing birds were infected with both parasite and vector, but we have little evidence to back up this claim. The various DNA lineages of *Haemoproteus multipigmentatus* found infecting Galapagos doves were also detected in continental South American dove species (Santiago-Alarcon et al. 2010). These lineages do not appear to have diversified recently from one single lineage, which would be evidence of differentiation within the Galapagos archipelago since arrival. Instead, it seems plausible that this parasite was introduced recently and multiple times to Galapagos, probably via a vagrant dove host like the eared dove (*Zenaida auriculata*) or with introduced rock doves, both of which have been found to be hosts of *H. multipigmentatus* (Santiago-Alarcon et al. 2010; Valkiunas et al. 2010). Rock doves were introduced to Galapagos in the early 1970s and are now completely eradicated from the islands, but *H. multipigmentatus* was also detected in rock doves once collected in Galapagos (P. Parker, personal communication). Interestingly, rock doves in continental areas are infected with the hippoboscid fly *Pseudolynchia canariensis*, while the flies found infecting Galapagos doves belong to the species *Microlynchia galapagoensis*, so the role of the supposed vector of *H. multipigmentatus* in Galapagos in these multiple colonization events is currently unknown.

In contrast, Galapagos frigatebird species are infected with just one lineage of *Haemoproteus iwa*, which is probably vectored by the hippoboscid fly, *Olfersia spinifera* (Levin et al. 2011). Vector confirmation for both *M. galapagoensis* and *O. spinifera* involved DNA amplification of *Haemoproteus* from fly thorax without amplification of avian host DNA, indicating developing parasite (sporozoite) in the thorax (Valkiunas et al. 2010; Levin et al. 2011). Although Galapagos frigatebirds are genetically isolated from frigatebirds in the rest of their tropical range (Hailer et al. 2010; see Chap. 2), only one *Haemoproteus iwa* lineage has ever been recovered both in Galapagos birds and frigatebirds in other locations (Levin et al. 2011). Magnificent frigatebirds colonized the Galapagos archipelago approximately 247,200 years ago (95% confidence intervals: 82,800–647,400) (Hailer et al. 2010). Using the estimated DNA sequence divergence rate for the hemosporidian cytochrome *b* gene (1.2% per million years, Ricklefs and Outlaw 2010), the lack of sequence divergence within Galapagos is consistent with the parasite and vector arriving with the colonizing host (Levin et al. 2011). However, it is still possible that the parasite and fly vector are more recent arrivals. Frigatebirds are philopatric to their breeding site, but travel great distances during the non-breeding season (Dearborn et al. 2003; Weimerskirch et al. 2006). We know that hippoboscid flies do regularly move between host individuals at a local scale; interestingly, the flies that do move between birds are less likely to be infected with *Haemoproteus iwa* (Levin and Parker 2014). In order to fully understand the colonization history of hippoboscid fly vectors in Galapagos, large-scale phylogenetic and phylogeographic studies of *Haemoproteus* parasites, bird hosts, and hippoboscid flies are needed, with an effort to estimate arrival dates where possible.

3.4 Anthropogenic Colonization

The introduction of new parasites and disease vectors due to human activities represents a major threat to Galapagos Islands biodiversity (Wikelski et al. 2004; Gottdenker et al. 2005; Whiteman et al. 2005; Kilpatrick et al. 2006b). This threat has substantially increased in the last two decades due to the rapid growth of the resident and visitor population associated with the booming tourism industry (Peck et al. 1998; UNESCO 2006; UNESCO 2010). As for isolated islands elsewhere, the principal routes of introduction of disease vectors and parasites to the Galapagos Islands are transport by boat and airplanes (Wikelski et al. 2004; Causton et al. 2006; Kilpatrick et al. 2006b).

There are two airports in Galapagos (Baltra and San Cristobal Islands) connecting the archipelago to Guayaquil and Quito in mainland Ecuador, and one cargo route from Guayaquil stopping at San Cristobal, Santa Cruz, and Isabela Islands (Fig. 3.5). Private jets have flown to Galapagos directly from places as varied as Florida, Brazil, and the Middle East without any systematic quarantine measures (Cruz Martinez and Causton 2007). In 2011, more than 2800 commercial flights, 200 cargo ships, and 400 privately-owned jets or boats made trips to the Galapagos Islands (Galapagos quarantine and inspection system-SICGAL annual report 2011). A quarantine and inspection system (SICGAL) is in place to control the movement of goods to and between islands (Causton et al. 2006), but presently SICGAL does

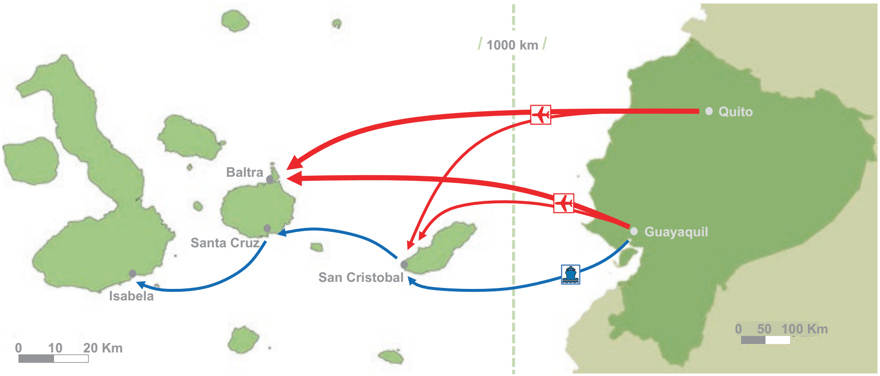

Fig. 3.5 Map showing shipping and air traffic routes connecting the Galapagos Archipelago to mainland Ecuador. Most flights (~70%, representing over 2000 flights a year) arrive at Baltra airport

not have the capacity to effectively implement the procedures that are necessary to prevent carriage of stowaway invertebrates by plane or boat to (and within) the Galapagos Archipelago (UNESCO 2006; UNESCO 2010).

Human activities have directly affected the health of the native Galapagos fauna through deliberate or accidental killing and injuries by humans or by other species they have introduced since the discovery of the archipelago (Dowler et al. 2000; Gottdenker et al. 2008; Poulakakis et al. 2008; Denkinger et al. 2015). Beyond physical injuries, human presence can also have a direct stress-related effect on the health of Galapagos wildlife. Notably, it has been shown that even low levels of human disturbance like ecotourism can increase levels of the stress hormone corticosterone in marine iguanas and modify some of their immune response capacities such as bacterial killing ability or cutaneous wound healing (French et al. 2010). In Galapagos sea lions, the immune activity and body condition of individuals living in the urban colony of Puerto Baquerizo Moreno on San Cristobal Island differ from those in the colonies located in the protected zones of the National Park (Brock et al. 2013). Human-related impact on this urban sea lion colony includes close contact with humans and domestic animals, contact with pollutants from sea vessels, and with bacteria of human origin (Wheeler et al. 2012; Brock et al. 2013; Denkinger et al. 2015).

Free-living, motile parasites that can survive a long time in the environment may have arrived directly to the Galapagos archipelago by hitchhiking on human transports. The parasitic botfly *Philornis downsi* represents the most likely case of such stowaway introduction in the archipelago. This fly lays eggs in bird nests and the larvae feed on blood of nestlings, with negative consequences on nestling survival (Fessl et al. 2006; Koop et al. 2011). *Philornis downsi* was introduced to the Galapagos Islands from mainland Ecuador in the 1960s (Causton et al. 2006; Bulgarella et al. 2015), maybe with imported fruit or in the cargo holds of planes. Alternatively, it could have been introduced with infected vertebrate hosts, for example chickens or pigeons, or with their nest material. The case of this fly and its impact on Galapagos avifauna will be discussed in detail in Chap. 9.

3.4.1 Colonization with Introduced Vertebrate Host

Most invasive parasites detected in the native Galapagos terrestrial vertebrate fauna probably originated from introduced vertebrate hosts, especially domestic animals. Parasites introduced with chickens have been particularly well studied. Several surveys carried out on chickens from inhabited islands of the archipelago (Gottdenker et al. 2005; Soos et al. 2008; Deem et al. 2012) indicated infection by *Mycoplasma gallisepticum*, a globally distributed bacterium that causes chronic respiratory disease in poultry and conjunctivitis in wild birds (Williams et al. 2002), and by nine different types of viruses, including the contagious Newcastle disease (avian paramyxovirus 1) that infects many domestic and wild avian species (Alexander et al. 2012). Antibodies to Newcastle virus and to an adenovirus

(Adenovirus-2) were also detected in Galapagos finches on Floreana Island, suggesting potential spillover from poultry to wild birds (Deem et al. 2012). Multiple nematode, cestode, trematode, and protozoan parasites were also identified, including a *Dyspharynx* nematode that has been associated with mortalities in Galapagos dark-billed cuckoos (Gottdenker et al. 2005). Marek's disease, caused by a herpesvirus, is also present and caused mortality in Galapagos domestic poultry in 1995/1996, but risks for native Galapagos avifauna are considered low because there are no susceptible native galliform species in the archipelago (Miller et al. 2001; Gottdenker et al. 2005).

Galapagos poultry are also infected by avian pox, caused by an avipoxvirus of the fowlpox lineage (Gottdenker et al. 2005). However, this strain of avipoxvirus seems restricted to chickens, whereas other strains of the canarypox lineage have been affecting the Galapagos passerine birds since at least 1899 (Thiel et al. 2005; Parker et al. 2006, 2011). This canarypox virus lineage can have a major impact on the survival of some endemic passerine populations during stressful environmental conditions like El Niño events (Curry and Grant 1989). Examination of museum specimens suggested that this avipoxvirus arrived to the archipelago in the late 1890s, possibly with early settlers, or via a natural colonization with migrating passerines like Bobolinks (see Sect. 3.2) (Parker et al. 2011). Despite the difference in hosts between fowlpox and canarypox viruses, the sympatry of the two pox lineages in some areas may allow for recombination and virulence alteration of avian pox viruses in Galapagos (Thiel et al. 2005). The transmission of avian pox in the archipelago is probably facilitated by endemic and introduced mechanical vectors (see sections on vectors above and below).

Importation of broiler chickens for industry in Galapagos increases the risk of introducing avian parasites to the archipelago. Strict biosecurity protocols are not implemented in Galapagos broiler houses, permitting direct contact of wild birds with poultry (Gottdenker et al. 2005). However, backyard chickens may represent a greater threat of disease spillover to Galapagos wildlife than broiler chicken, because they harbor more parasites and are more frequently in contact with wildlife (Soos et al. 2008).

Rock doves introduced to the Galapagos Islands facilitated the arrival of the flagellate protozoa *Trichomonas gallinae*, and the subsequent infection of Galapagos doves by this parasite (Wikelski et al. 2004). Domestic cats and dogs also brought their parasites with them to the Galapagos archipelago. High prevalence (20–60%) of canine distemper virus and the dog heartworm *Dirofilaria immitis* have been detected in Galapagos dog populations, which has led to major concerns of spillover to marine mammals (Levy et al. 2008; Diaz et al. 2016). Of the parasites infecting cats in Galapagos Islands, the high prevalence of *Toxoplasma gondii* represents the most significant threat to the endemic wildlife (Levy et al. 2008). This protozoan parasite infects all warm-blooded animals, including humans, but felid species are their only definitive hosts, necessary for their sexual reproduction (Tenter et al. 2000). Infected cats can notably transmit the parasite to other hosts via ingestion of contaminated feces. Infection by *T. gondii* was observed in many species of birds across the globe (Dubey 2002), including the endemic bird ‘Alala from Hawaii

(Work et al. 2000). In Galapagos, low prevalence (1–8%) of antibodies to *T. gondii* was detected in Galapagos penguins and flightless cormorants (Deem et al. 2010).

Apart from the potential spread of parasites through the introduced domestic species, a few introduced species that now live in the wild could also have brought parasites to the Galápagos with them. The smooth-billed ani and the cattle egret are abundant birds in Galapagos that were brought by humans and could represent a source of new parasites, but they have not yet been well studied in this respect.

3.4.2 Anthropogenic Introduction of Vectors

Several disease vectors have been introduced by humans to the Galapagos archipelago, but, for most of them, the exact mode and frequency of introduction has not been studied in detail. The yellow fever mosquito, *Aedes aegypti,* has been present in urbanized areas of Santa Cruz and San Cristobal Islands since 2001, and is associated with cases of dengue fever since then (Causton et al. 2006). The biting midge *Culicoides pusillus,* a potential vector for blue tongue virus, is established in Santa Cruz Island since at least 1964 (Causton et al. 2006). The blackfly, *Simulium bipunctatum*, vector of the river blindness worm, was detected in 1989 and is distributed on three islands, including the uninhabited Santiago Island (Causton et al. 2006). Lastly, the southern house mosquito, *Culex quinquefasciatus*, vector of multiple parasites such as avian malaria parasites and West Nile virus, was first recorded in 1985 in Santa Cruz, and is now distributed in all inhabited islands of the archipelago (Peck et al. 1998; Causton et al. 2006).

All these vectors have restricted distribution in the archipelago because they require fresh water for breeding, which is mostly accessible in the humid areas of the islands and in human-inhabited areas, where open fresh water tanks and man-made cavities (e.g., discarded tires and containers) containing fresh water are readily available (Fig. 3.6). The only introduced disease vector that has been studied in further detail is *C. quinquefasciatus*.

3.4.2.1 The Southern House Mosquito (*Culex quinquefasciatus*): On-Going Introduction of a Major Disease Vector

Culex quinquefasciatus is a member of the globally distributed *Culex pipiens* species complex, and is found in tropical and sub-tropical regions where it breeds in freshwater with high organic content, depositing egg rafts on the water surface. It is extremely successful in human-inhabited areas because of the abundance of stagnant freshwater bodies, but it also breeds in forest environments. It is an important vector for a wide variety of diseases, such as West Nile virus (Sardelis et al. 2001), filariasis (Farid et al. 2001), avian pox and avian malaria (van Riper et al. 1986; Fonseca et al. 2000). It feeds readily on mammals and birds, so it can play the role of a bridge vector, notably for the transmission of West Nile virus (Sardelis et al.

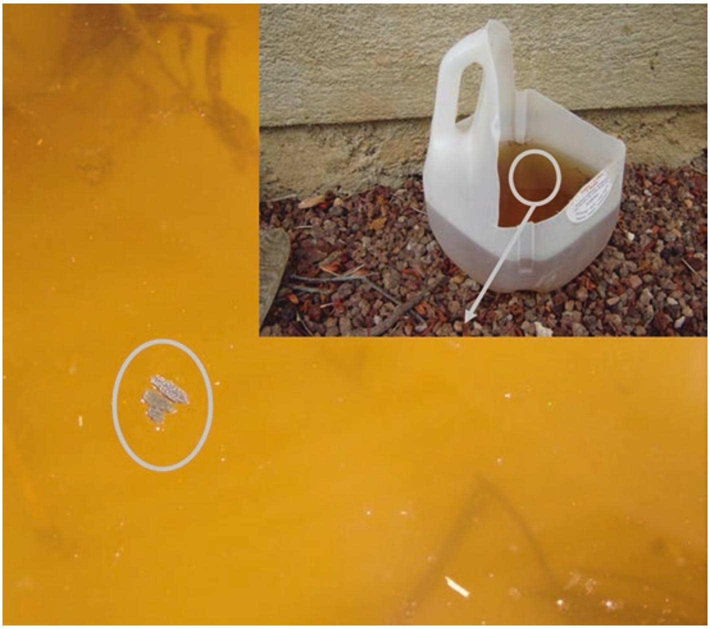

Fig. 3.6 Eggs of the introduced southern house mosquito (*Culex quinquefasciatus*) deposited in an abandoned plastic container filled with water (Photos: Arnaud Bataille)

2001). The nineteenth century introduction of this vector and of avian pox in Hawaii followed by a later introduction of avian malaria is thought to be the main reason for the dramatic decline of Hawaiian endemic birds throughout the twentieth century (Warner 1968; van Riper et al. 1986, 2002).

The presence of *C. quinquefasciatus* in the Galapagos Islands is considered to be a serious threat to its endemic fauna because of the role of this mosquito in wildlife disease transmission elsewhere (Whiteman et al. 2005; Causton et al. 2006). Multiple parasites vectored by this mosquito are already present in Galapagos, most notably avian pox viruses, *Plasmodium* parasites, and the nematode *Dirofilaria immitis* (see Sect. 3.4.1). However, its exact role in the transmission of these parasites remains unclear. The capacity of the Galapagos *C. quinquefasciatus* to transmit parasites has only been demonstrated for West Nile virus (Eastwood et al. 2011). Additionally, it is worth noting that a pool of 30 *C. quinquefasciatus* heads tested positives to avian pox virus in a PCR assay (Bataille A, Cruz M, Cedeno V, Cunningham AA, Goodman SJ, unpublished data), supporting its potential role in the mechanical transmission of this virus (Thiel et al. 2005).

A worldwide genetic survey of *C. quinquefasciatus*, including samples from the Galapagos Islands, was conducted using microsatellite markers (Fonseca et al. 2006). The Galapagos samples were genetically very similar to specimens from mainland Ecuador, supporting the idea of a recent colonization of the archipelago from this country. However, the study included only a small number of samples from one island (Santa Cruz), which was insufficient to fully understand the history of its presence on the archipelago or the risks of current and future introductions.

During the 2006–2007 airplane monitoring program, eight live *C. quinquefasciatus* mosquitoes were collected in airplanes arriving in Baltra and San Cristobal airports, evidence of their on-going introduction to the archipelago (Bataille et al. 2009b). The same authors sampled *C. quinquefasciatus* specimens across the Galapagos Islands and in mainland Ecuador, and used microsatellite markers to further assess the genetic similarity between the mosquito populations in the archipelago and mainland Ecuador, and to determine the pathways and frequency of introduction of this mosquito from the mainland to the archipelago. They showed that the *C. quinquefasciatus* populations in Baltra and San Cristobal (the two islands hosting airports connected to mainland Ecuador) were genetically more similar to mainland mosquito populations than to populations from Santa Cruz, Isabela, or Floreana Islands (Bataille et al. 2009b). Such a pattern is most likely the result of frequent introductions of mosquitoes via airplane, and of their successful integration into already-established populations.

Culex quinquefasciatus could also arrive in the archipelago with cargo boats arriving to Santa Cruz, San Cristobal, and Baltra islands. However, Bataille et al. (2009b) did not observe a strong genetic similarity between *C. quinquefasciatus* populations of Santa Cruz Island and mainland Ecuador, suggesting that *C. quinquefasciatus* introduction by boat is much less important than by airplane. Although airplane disinfection has been implemented for commercial flights bound to Galapagos since 2007 following World Health Organization guidelines, the increase in flights to the archipelago associated with tourism development still represents a major risk of parasite introduction with infected disease vectors.

3.5 Conclusions and Future Directions

Our understanding of parasite and vector colonization in Galapagos is incomplete. However, there are several well-studied examples (e.g., mosquitoes, avian hemosporidians, avian pox), which emphasize that all routes of introduction including natural colonization, colonization with a vertebrate host (a colonizer or migrant/vagrant), and anthropogenic colonization have been documented. We know the most about colonization of a few organisms of conservation concern, such as the mosquito species known as disease vectors elsewhere in their distribution. We lack specific information on colonization for the majority of parasites identified in Galapagos (see Table 3.2) and therefore can only speculate on arrival mode and evolutionary history.

In order to properly study parasite and vector colonization, research must extend to continental sister taxa or, in cases of non-endemic species, research must include organisms sampled outside their Galapagos range. The best approaches for studying colonization include detailed phylogeographic and population genetic approaches.

When possible, researchers should sample the entire parasite community in and on Galapagos animals and their closest continental relatives. By sampling parasite assemblages, we can reconstruct more accurate hypotheses about parasite arrival and divergence within Galapagos. For example, by examining all species of lice and mites found on the Galapagos flycatcher and their most closely related continental sister taxa, the Brown-crested flycatcher, Sari et al. (2013) concluded that the suite of ectoparasites probably arrived with the ancestor of the Galapagos flycatcher and that only one mite species had diverged in morphology since arrival to Galapagos. Sampling only the divergent mite could have led to a different conclusion. Furthermore, vertically transmitted and closely host-associated parasites can be used as additional evidence for revealing host evolutionary history (Whiteman and Parker 2005). Thus, studying parasite colonization adds more information about the evolutionary history of Galapagos than simply an answer to how that particular parasite colonized the islands.

When inferring whether a parasite arrived by natural colonization or by human introduction, it is important to predict which ones may represent a greater threat to the Galapagos native fauna. Endemic fauna have been isolated in the archipelago for a long time, and may have lost their ability to mount immune responses against recently introduced parasites. So knowledge about arrival and transmission of introduced parasites is essential and urgent for proposing conservation strategies and the prevention management in Galapagos.

Continued—and perhaps expanded—monitoring programs are needed to prevent further human-aided parasite introduction. Generalist parasites with robust free-living stages or free-living vectors are of greatest concern, as they could be brought in on boats or in cargo holds of planes. Host-specific parasites are of less concern because their most plausible route of introduction is with the host, and even if they arrived, they are less likely to establish on a novel host. There is still concern about the introduction of parasites via migratory birds, but there is little that can be done to prevent parasite spread from migratory sources, except regular avian screening (see Fig. 3.7). For example, there is concern about the potential arrival of *Plasmodium relictum*, the pathogenic hemosporidian species that has contributed to the decline and extinction of many Hawaiian honeycreepers. *Plasmodium relictum* could arrive to Galapagos via an infected bird, but in order for the parasite to establish, a competent vector is needed. Unfortunately, the vector of this lineage in Hawaii, *Culex quinquefasciatus*, is well established in Galapagos. Preventing the colonization of *P. relictum* would require eliminating the introduced *C. quinquefasciatus*, which is not a simple task. Both *C. quinquefasciatus* and native *Aedes taeniorhynchus* mosquitoes are competent vectors for West Nile Virus, which has not yet colonized the archipelago.

Collaboration should be a top priority as more research is conducted on parasites in Galapagos. Research teams working in Galapagos do not always interact or coordinate during their research expeditions. There are many local and international groups collecting samples in the islands and many of these samples could be used for multiple purposes, beyond the original reason for the collection. For example, blood collected for a population genetic study could be screened for hemosporidian

Fig. 3.7 Screening domestic and migrating ducks for diseases threats to Galapagos fauna such as avian influenza (Photos: Arnaud Bataille)

parasites. Because it is expensive and time-intensive to sample many islands within the Galapagos, coordination of research among different teams can improve sampling effort. Increased communication, better database compilation and sharing, and more comprehensive sampling could vastly improve our knowledge about the parasites in the Galapagos archipelago and how they got there.

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Part II
Island Syndromes

Chapter 4
Genetic Diversity in Endemic Galápagos Birds: Patterns and Implications

Jennifer L. Bollmer and Benjamin D. Nims

Abstract Due to their smaller sizes and isolation, island populations generally have reduced genetic variability, which can have negative fitness consequences. The Galápagos Islands have played a unique and important role in our understanding of evolution, and the population genetics of bird species native to the islands is relatively well studied. Native Galápagos bird species exhibit a range of genetic patterns at neutral loci. For example, hawk and mockingbird population genetic variability is closely correlated with island size, demonstrating the effect of genetic drift, whereas gene flow has mitigated the effect of drift in dove and finch populations, resulting in higher genetic variability. Similarly, Galápagos seabirds exhibit a range of patterns, with some having greatly reduced variation compared to relatives outside of Galápagos (e.g., magnificent frigatebirds, penguins) and others having relatively high genetic variability (e.g., great frigatebirds). Published studies of major histocompatibility variability in hawks and penguins show a pattern of reduced variability at functional loci for Galápagos species compared to mainland congeners. Research has also demonstrated a relationship between genetic variability and fitness in some Galápagos species. Galápagos hawks have weaker innate immune function and higher louse loads than their more heterozygous mainland congener, and medium ground finches with higher heterozygosity are more likely to survive and breed. In contrast, no relationship between inbreeding and innate immune function or ectoparasite load was detected for mockingbirds. Further study of the population genetic dynamics of these species will continue to better inform management practices in the face of evolving threats.

Keywords Genetic drift • Genetic variation • Neutral loci • Selection • Major histocompatibility complex

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4.1 Genetic Variability: Causes and Consequences

The field of evolutionary biology has provided scientists and conservationists with the context, tools, and data to answer fundamental questions about the diversity of life on Earth, both past and present. Through the study of population genetics, we gain further insight into the evolutionary processes that lead to the survival of populations and the emergence of new species. At the heart of this endeavor is our fundamental knowledge of the processes that create, maintain, or eliminate genetic variation. As we gain a better understanding of these processes, we can begin to unravel how heritable variation, in the context of various neutral and selective pressures in different environments, leads to genotypes and phenotypes that affect a species' survival.

4.1.1 Factors Shaping Genetic Diversity

Genetic variation is the foundation upon which evolutionary processes work. The capacity of a species to adapt to changing environments is largely dependent on polymorphisms present in the gene pool. The level of genetic variation found in a population is the result of a number of factors, such as mutation rate, selection, genetic drift, and gene flow (Bohonak 1999). Mutation generates the variation upon which the other forces act. Mutations can be neutral or have fitness consequences, and they can be as small as point mutations of single bases or cause the duplication or deletion of entire genes or even chromosomes. At functional loci, selection may act to decrease or increase population genetic variability. For example, a selective sweep (strong positive section) decreases population variability by increasing the frequency of an advantageous mutation toward fixation, as well as allowing closely linked neutral or even slightly deleterious alleles to hitchhike toward fixation with it (Berry et al. 1991). Purifying (negative) selection also decreases population variability by removing mutations that are deleterious. For example, purifying selection has been demonstrated to weed out nonsynonymous mutations in mtDNA (Stewart et al. 2008). In contrast, balancing selection increases genetic diversity through several mechanisms, including negative frequency-dependent selection (or rare allele advantage; Takahata and Nei 1990) and overdominance (or heterozygote advantage; Doherty and Zinkernagel 1975). Evidence for balancing selection includes diversity found at the major histocompatibility complex (MHC) in vertebrates (reviewed in Bernatchez and Landry 2003; Garrigan and Hedrick 2003).

The rate at which these factors affect variability depends also on stochastic demographic events. Small populations lose variability faster than large populations due to the stronger effects of genetic drift (Nevo et al. 1984). The positive relationship between population size and genetic variability is well known (Frankham 1996). Events such as population bottlenecks can cause a loss in allelic variation (Leberg 1992; Groombridge et al. 2000); however, the extent of the impact on variation depends on the bottleneck's severity and longevity. Population subdivision can exacerbate the loss of genetic variation. It has been established that fragmentation that results in small isolated populations can lead to loss of diversity (Templeton et al. 1990). In contrast, gene flow can mitigate the effects of genetic drift in a population by restoring lost alleles or adding new alleles from source populations (Slatkin 1985). Therefore, demographic history, vagility, and past stochastic environmental events are all relevant in understanding population genetic variability and evolution within a species.

4.1.2 Fitness Consequences of Diversity

Genetic variability represents the potential a species has to adapt to a changing environment; thus, it has fitness consequences at the individual, population, and even species level. There is a large literature investigating the relationship between a loss in genetic variability and decreased fitness (inbreeding depression) at traits such as body condition, survival, and reproductive success (Crnokrak and Roff 1999; Keller and Waller 2002; Reed and Frankham 2003). Loss of genetic diversity has also been associated with increased disease susceptibility (e.g., Penn et al. 2002; Acevedo-Whitehouse et al. 2003). Inbreeding is predicted to result in an increased risk of extinction (O'Grady et al. 2006), and some studies have found an association between decreased genetic variability and extinction in wildlife (Frankham 1995; Saccheri et al. 1998). While demographic factors may be of more immediate concern when managing endangered populations (Lande 1988), it is also important to understand population genetic factors to better inform conservation decision-making (Frankham et al. 2002).

4.1.3 Genetic Diversity in Island Populations

Island archipelagos provide exceptional opportunities to examine forces affecting genetic variation and evolution. Island populations are discrete, facilitating investigation of the relative strengths of genetic drift, gene flow, and selection in shaping genetic variation. A common characteristic of island populations is reduced genetic variability. Island populations are usually smaller than mainland populations, being limited in size by the area of the island they inhabit. Studies of natural island populations often find a robust relationship between genetic variation and island size (Frankham 1997), indicating the strong influence of genetic drift. At foundation, island populations may undergo a genetic bottleneck (founder event) if the colonizers are few in number and carry only a subset of the genetic variability present in the source population. This is particularly true when the islands are far from a source of colonists, and the colonizing events themselves are rarer than for islands closer to continental landmasses. Rare alleles are especially likely to be lost, reducing the evolutionary potential of the population. Subsequent to foundation, island species may continue to experience long-term genetic drift in small populations. Island endemics often have less variability than non-endemic island species (Frankham 1997), presumably because of continued drift as well as selection. Water acts as an effective barrier to gene flow for many species, and island populations are often more isolated and differentiated from each other than mainland populations (Frankham 1997), further exacerbating loss of genetic variability. Island populations exist in relatively simple ecological communities, facilitating our ability to study the relationships between genetic variation and fitness traits, including disease resistance.

The Galápagos Islands have played a unique and central role in the development of evolutionary theory. Their isolation has historically limited the impact of human activity, leaving the fauna relatively intact, and recent human activity has been limited by their designation as the Galápagos National Park and Marine Reserve by the government of Ecuador in 1959. The presence of multiple islands of varying size, along with the varying number of subpopulations of different species that range over these islands, offers an ideal location in which to study factors affecting genetic diversity. Scientists have accumulated a wealth of data on the population genetics of vertebrates native to Galápagos. Population genetic studies continue to advance basic science as well as provide better information to managers tasked with preserving these species. While this unique ecosystem has for the most part avoided human-induced population and species reductions, there is no shortage of threats, ranging from invasive species to climate change, in an environment that impresses many as harsh (see Fig. 4.1). In particular, the threat of introduced diseases to the endemic fauna of Galápagos has received considerable attention (Wikelski et al. 2004; Parker and Deem 2012). The primary focus of this chapter is to explore patterns of genetic diversity within endemic Galápagos species, as well as the relationship between diversity and fitness traits where known.

4.2 Genetic Diversity at Neutral Loci in Galápagos Avifauna

The Galápagos Islands harbor a diverse array of bird species. Approximately 56 of the 178 recorded species are endemic or native residents of the archipelago (Jiménez-Uzcátegui et al. 2016), having estimated colonization times as recent as less than 200,000 years ago (Band-rumped storm petrels, Smith and Friesen 2007) to as long as a few million years ago (Galápagos mockingbirds, Arbogast et al. 2006, see Chap. 2). The majority of land birds are endemic species or subspecies, while seabirds residing in Galápagos have a lower rate of endemism, likely due to their pelagic life-histories. Neutral genetic diversity within the Galápagos avifauna has been well characterized (Table 4.1). The extent of the loss of genetic variability predicted by island theory depends, to a large extent, on effective population size and degree of inter-island gene flow. These in turn are affected by taxonomic traits such as the niche a species fills and its ability to fly across wide stretches of water.

Fig. 4.1 Sullivan Bay on Santiago Island. Photo by JLB

4.2.1 Patterns Within Land Birds

Galápagos hawks (*Buteo galapagoensis*; Fig. 4.2) have lower neutral variability than their closest mainland relative, the Swainson's hawk (*Buteo swainsoni*), at every marker analyzed (Bollmer et al. 2005, 2006, 2011). At multilocus minisatellites, unrelated individuals in outbred populations typically share 20–30% of their bands (Parker Rabenold et al. 1991). In the Galápagos hawk, populations averaged 69–96% band-sharing, with the most inbred populations having multiple individuals with identical banding patterns (Bollmer et al. 2005). In contrast, a small sample of Swainson's hawks ($n = 8$) had 37% band-sharing. At almost 3 kb of mtDNA, 122 Galápagos hawks sequenced exhibited only seven haplotypes across all nine islands of their range, compared to 12 in the 29 Swainson's hawks sampled on their South American wintering grounds, presumably representing multiple breeding locations in North America; seven of the nine Galápagos hawk populations were fixed for a single haplotype (Bollmer et al. 2006). Lastly, at 13 microsatellite loci, Galápagos hawk populations had lower average heterozygosity than the Swainson's hawk ($H_o = 0.03$ and 0.87, respectively). The low variability in the Galápagos hawk does not appear to be the result of a recent bottleneck (Bollmer et al. 2011), but rather a loss of variation at foundation. High background similarity among populations at minisatellite loci (despite a lack of gene flow; Bollmer et al. 2005; Koop et al. 2014)

Table 4.1 Summary of studies investigating neutral genetic diversity in Galápagos bird species

Taxonomic Group	Species	Genetic markers	Pattern	Reference
Land birds	Galápagos dove (*Zenaida galapagoensis*)	5 microsatellite loci	Within-population genetic diversity did not differ among islands; allelic richness similar to mainland species; high gene flow among island populations	Santiago-Alarcon et al. (2006)
	Galápagos finches (*Geospiza, Certhidea, Camarhynchus*, *Cactospiza*, spp.)	14–16 microsatellite loci	High levels of gene flow among islands, reduced levels between central and northern islands; higher rates of interspecific admixture on peripheral islands than central islands; reduced variation and higher genetic differentiation among *Certhidea* populations	Petren et al. (2005) and Farrington et al. (2014)
	Galápagos flycatcher (*Myiarchus magnirostris*)	mtDNA cytb (907 bp)	Low nucleotide and haplotype diversity within island populations (did not correlate with island size); strong between-island genetic structuring indicated by AMOVA	Sari and Parker (2012)
	Galápagos hawk (*Buteo galapagoensis*)	Multilocus minisatellites, 20 microsatellite loci, 2 mtDNA genes (911 bp)	Low levels of genetic diversity at all loci examined; genetic variation closely correlated to island area; strong between-island genetic structuring	Bollmer et al. (2005, 2006, 2011) and Koop et al. (2014)

(continued)

Table 4.1 (continued)

Taxonomic Group	Species	Genetic markers	Pattern	Reference
	Galápagos mockingbirds (*Mimus* spp.)	16 microsatellite loci	Within-population genetic diversity correlated with island size; low gene flow; genetic differentiation increased with geographical distance; temporal F_{ST} higher within smaller populations	Hoeck et al. (2010)
	Yellow warbler (*Setophaga petechia aureola*)	11 microsatellite loci; mtDNA control region (330 bp)	Relatively high genetic diversity at both marker types; moderate genetic differentiation among islands; gene flow generally from southeast to northwest	Chaves et al. (2012)
Seabirds	Nazca booby (*Sula granti*)	8 microsatellite loci; 3 mtDNA genes (2–2.1 kb)	Population genetic diversity similar across islands; recent bottlenecks detected in three of five colonies; significant differentiation among some colonies, with three genetic clusters most likely	Levin and Parker (2012)
	Great frigatebird (*Fregata minor*)	8 microsatellite loci; 3 mtDNA genes (2–2.1 kb)	Population genetic diversity similar across islands; no evidence of recent bottlenecks; weak to no genetic structuring among populations at both markers	Levin and Parker (2012)

(continued)

Table 4.1 (continued)

Taxonomic Group	Species	Genetic markers	Pattern	Reference
	Magnificent frigatebird (*Fregata magnificens*)	8 microsatellite loci; 3 mtDNA genes (1.6 kb); nuclear introns (1.6 kb)	Galápagos population had lower genetic variability than and was genetically distinct from the other Atlantic and Pacific populations sampled at all markers; little genetic structuring among non-Galápagos populations	Hailer et al. (2011)
	Galápagos petrel (*Pterodroma phaeopygia*)	6 microsatellite loci; mtDNA ATPase (650 bp)	Strong inter-island genetic structuring at both marker types	Friesen et al. (2006)
	Galápagos cormorant (*Phalacrocorax harrisi*)	5 microsatellite loci	Levels of genetic diversity did not differ among subpopulations; significant genetic structuring among subpopulations, especially between islands; pattern of isolation-by-distance	Duffie et al. (2009)
	Galápagos penguin (*Spheniscus mendiculus*)	5 microsatellite loci	Low genetic diversity overall; levels of genetic diversity did not differ among subpopulations; no genetic structuring among subpopulations	Nims et al. (2008)

and fixation for the same mitochondrial haplotypes in multiple populations (Bollmer et al. 2006) support this. As an apex predator, hawk populations are relatively small compared to most other species inhabiting the same islands, and the lack of gene flow among populations augments the effect genetic drift has within populations. As a result, hawk genetic variability is closely correlated with island area ($r = 0.844$, $p = 0.008$; Bollmer et al. 2005; Fig. 4.3a).

In a comprehensive study of the population genetics of the four Galápagos mockingbird species (*Mimus* spp.), Hoeck et al. (2010) investigated genetic diversity using contemporary samples from nearly the entire species range as well as historical

Fig. 4.2 Adult Galapagos hawk *Buteo galapagoensis* on Santiago Island. Photo by JLB

samples obtained from the museum collection at the California Academy of Sciences (CAS), which collected them in 1899 and 1905–1906. At 16 microsatellite loci, Hoeck et al. found that diversity was significantly positively related to island size (Fig. 4.3a) and negatively related to island age, with mean population H_e ranging from 0.072 to 0.585. Overall, contemporary within-population genetic diversity was not different from historic diversity (although a subset of populations either lost or gained diversity), suggesting populations are generally in migration-drift equilibrium at these loci. However, temporal F_{ST} calculations were significantly negatively correlated with island size ($r^2 = 0.93$, $p < 0.0001$), with populations on smaller islands showing greater change over time than larger islands (Figs. 4.3 and 4.4); this is consistent with predictions of genetic drift. Similar to the hawks, mockingbirds also exhibit extensive genetic differentiation among island populations, especially between species (Hoeck et al. 2010).

The Galápagos flycatcher (*Myiarchus magnirostris*) shows similarly low diversity at the 907 bp cytb mtDNA region sequenced by Sari and Parker (2012). In 154 samples from seven islands, they found 12 haplotypes with limited divergence; there was one common haplotype, and nine similar haplotypes were rare and present on one island each. Sequences had low nucleotide ($\pi = 0.00087$) and haplotype ($h = 0.4913$) diversity. However, genetic diversity was not correlated with island area or number of birds sampled on each island.

The subspecies of yellow warbler (*Setophaga petechia aureola*) endemic to Galápagos is common throughout the archipelago. Chaves et al. (2012) used both a

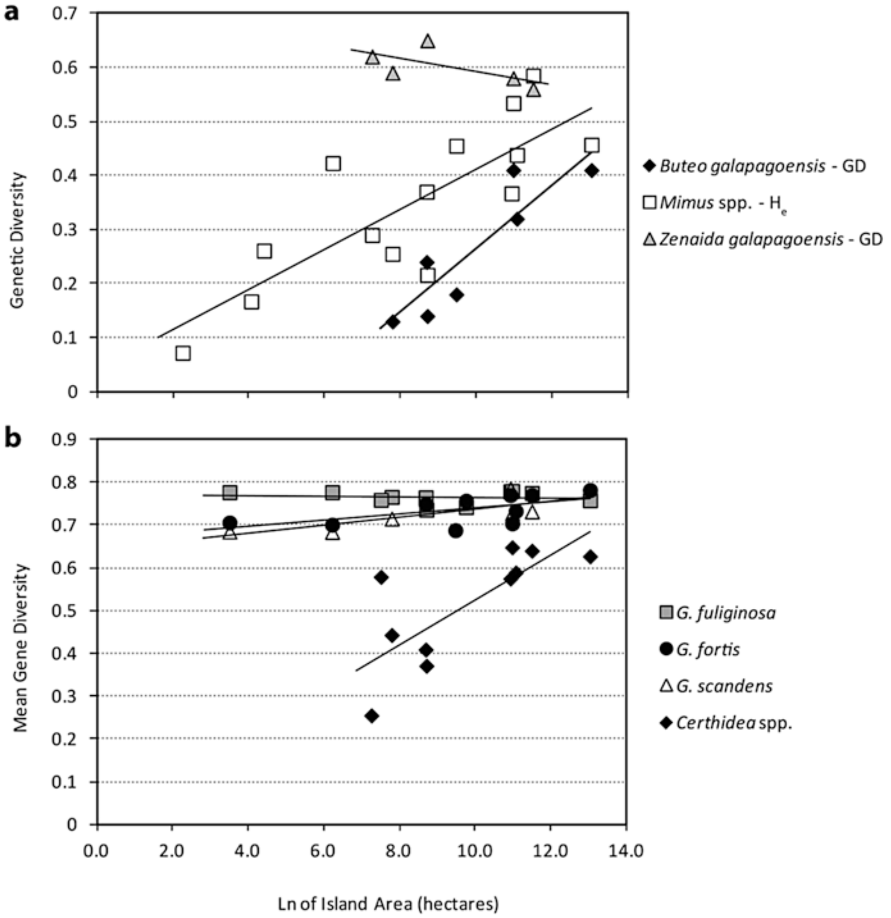

Fig. 4.3 (**a**)Microsatellite gene diversity (GD) or expected heterozygosity (H_e) values with trend lines for Galápagos hawks (*Buteo galapagoensis*; Bollmer et al. 2011), Galápagos mockingbirds (*Mimus* spp.; Hoeck et al. 2010), and Galápagos doves (*Zenaida galapagoensis*; Santiago-Alarcon et al. 2006), (**b**) Mean gene diversities with trend lines calculated from Farrington et al. (2014) microsatellite data using FSTAT for four Galápagos finch lineages

330 bp fragment of the mitochondrial control region and 11 microsatellite loci to describe the population genetics of this bird on nine islands. At the control region, 45 of 58 individuals sequenced shared a common haplotype, and there were eight haplotypes in total ($\pi = 0.0053$). The authors noted that the warbler mitochondrial diversity is higher than that found in two other bird species (Galápagos hawks and magnificent frigatebirds) with similar estimated arrival times to Galápagos. Chaves et al. found an overall microsatellite heterozygosity of 0.453 among 159 individuals genotyped. Genetic structuring at microsatellite loci was moderate, with most pairwise F_{ST} values being nonsignificant. A STRUCTURE analysis resulted in three clusters: Floreana, San Cristóbal, and the remaining seven islands sampled. Chaves

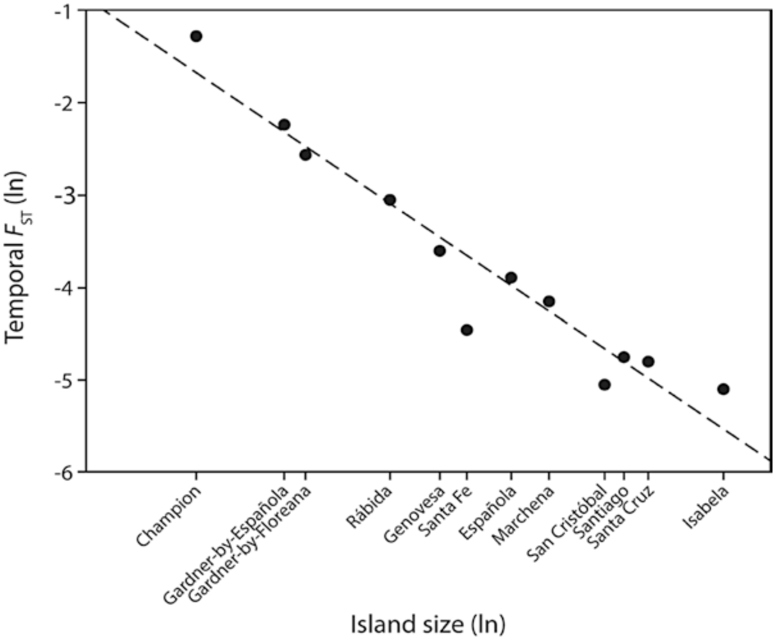

Fig. 4.4 Within-island temporal F_{ST} values between contemporary and historical populations of Galápagos Mockingbirds as a function of island size (Reproduced from Hoeck et al. (2010))

et al. found evidence for restricted gene flow, with a general pattern of unidirectional movement from the southeastern islands to the northwest, consistent with prevailing winds. The authors suggested that yellow warbler populations in Galápagos are in an early stage of diversification.

The Galápagos dove (*Zenaida galapagoensis*) appears to show higher genetic variability than the species above. At five microsatellite loci, Santiago-Alarcon et al. (2006) measured mean gene diversity (Nei 1973) ranging from 0.56 to 0.65 across the five island populations sampled. There was no significant difference among islands in allelic richness or gene diversity. In contrast to the hawk and mockingbird, the dove exhibits little genetic structuring (overall F_{ST} of 0.01, $p > 0.43$) and high levels of historic gene flow. The lack of a relationship between genetic diversity and island size (Fig. 4.3a) is likely due to the high gene flow. Santiago-Alarcon et al. (2006) noted that Genovesa and Española, the two smallest and most geographically isolated of the islands sampled, had populations with the largest genetic diversity and gene flow.

The most well-known of Galápagos' land birds are Darwin's finches. The adaptive radiation of the finch lineage has resulted in 15 recognized species, with five genera occurring in the archipelago: *Geospiza* (ground), *Camarhynchus* and *Cactospiza* (tree), *Platyspiza* (vegetarian), and *Certhidea* (warbler) finches. In a microsatellite analysis of cactus (*G. scandens*, *G. conirostris*), warbler (*C. olivacea*, *C. fusca*), and sharp-beaked ground finches (*G. difficilis*), Petren et al. (2005) found that only warbler finch heterozygosity was significantly positively related to island area, while the other two groups showed weaker trends. Gene diversities calculated from microsatellite data published by Farrington et al. (2014) showed similar patterns for four finch lineages (Fig. 4.3b). Petren et al. concluded that the warbler finches were most affected by drift, and inter-island gene flow likely mitigated the effect of drift in the *Geospiza* species. Unlike the other land bird lineages, the finch radiation has resulted in multiple finch species resident on each island, and interspecific introgression has complicated their population genetic patterns. There is genomic evidence for introgressive hybridization throughout the history of the finch radiation (Lamichhaney et al. 2015). Farrington et al. (2014) determined that interisland gene flow was lower between the central and northern island groups than within the groups, and interspecific admixture was higher on peripheral than central islands.

4.2.2 Patterns Within Seabirds

In a study of Great frigatebirds (*Fregata minor*) and Nazca boobies (*Sula granti*) at both microsatellite and mtDNA loci, Levin and Parker (2012) found contrasting patterns. Great frigatebirds had relatively high heterozygosity at eight microsatellite loci, 65% overall, and haplotype diversities at mtDNA averaged 0.655. They exhibited little to no genetic structure among the five populations sampled. Nazca boobies also had relatively high microsatellite heterozygosity (58%) and haplotype diversity (0.886). However, the boobies showed greater inter-island structuring. Nazca booby populations on Wolf and Darwin were not significantly differentiated, nor were those on Española and Genovesa, but the rest of the combinations had significant F_{ST} values. A STRUCTURE analysis predicted three genetic populations: Española and Genovesa, Wolf and Darwin, and San Cristóbal alone (Levin and Parker 2012).

Magnificent frigatebirds (*Fregata magnificens*) are highly mobile and distributed along the Atlantic and Pacific coasts of Central and South America in the tropics. Hailer et al. (2011) sampled frigatebird populations across the species range (including both the Pacific and Atlantic) and discovered that the Galápagos population (sampled on North Seymour Island) had the lowest genetic diversity of any of the nine sites sampled. Across three mtDNA regions, the Galápagos population had mean gene and haplotype diversities of 0.195 and 0.00012, respectively, compared to values ranging 0.421–0.927 and 0.00089–0.0187, respectively, in the other non-Galápagos populations. Allelic richness and heterozygosity at eight microsatellite loci were also lowest for the Galápagos population. Hailer et al. found that the Galápagos population was genetically differentiated from the other populations at both microsatellite and mtDNA, whereas the other populations showed little substructuring, even those sampled from different ocean basins. The lower genetic variability in the Galápagos population of magnificent frigatebirds is likely due to its isolation from its continental counterparts.

The Galápagos petrel (*Pterodroma phaeopygia*) is somewhat different from the above species. It is endemic and breeds in burrows in the highlands of five of the largest islands. Friesen et al. (2006) sampled individuals from all five islands and genotyped them at six microsatellite loci. Mean expected heterozygosities ranged from 0.43 to 0.51 across populations. Friesen et al. found evidence of genetic differentiation among populations, with private alleles occurring in all populations and F_{ST} values ranging from 0.07 to 0.26, all significant. This species is of special conservation interest in Galápagos; populations have been declining due to nesting habitat loss and the introduction of nest predators (Cruz and Cruz 1987).

4.2.3 Patterns Within Flightless Seabirds

Two of the seabirds endemic to Galápagos are flightless: the Galápagos penguin (*Spheniscus mendiculus*; Fig. 4.5) and the Galápagos cormorant (*Phalacrocorax harrisi*). The cormorants are generally restricted to the coastlines of Fernandina and western and northeastern Isabela, while the penguin's range also includes the rest of Isabela and colonies on Bartólome and Floreana. The Galápagos penguin and cormorant have undergone repeated poor reproductive periods and severe population fluctuations in association with decreased food availability during El Niño-Southern Oscillation (ENSO) events (Vargas and Wiedenfeld 2004). It is not surprising that studies measuring genetic diversity demonstrate the likely impact of these repeated genetic bottlenecks within each species. Across five microsatellite loci, Akst et al. (2002) reported observed heterozygosity (H_O) values of 3% in the Galápagos penguin compared to 46% in its congener the Magellanic penguin (*S. magellanicus*); similarly, the average number of alleles per locus was 2.0 versus 8.4, respectively. Further, Nims et al. (2008) examined the extent to which the Galápagos penguin exhibits genetic structuring within and among subpopulations throughout its range. Using five microsatellite markers (one of which was used by Akst et al. 2002), they reported an average H_O of 45%. While the average number of alleles per locus was similar at 2.8, the analysis at these additional loci indicated a trend of greater evenness among allele frequencies. The F_{ST} variant θ (Weir and Cockerham 1984) indicated no evidence for genetic differentiation between any of the five subpopulations sampled. These results indicate a low level of genetic diversity throughout the species and a seemingly high level of gene flow among subpopulations.

In contrast, analysis of genetic diversity in the Galápagos cormorant revealed a very different story. Duffie et al. (2009) identified 23 alleles at five microsatellite loci, with an average of 4.8 alleles per locus. Their findings show that the Galápagos cormorant population is genetically differentiated (global $F_{ST} = 0.097$) throughout its extremely limited breeding range on Isabela and Fernandina Islands. The level of population structure suggests that dispersal is limited, even in parts of the cormorant range where physical barriers do not appear to exist. Further, the authors state that low vagility, behavioral philopatry, or both may serve to promote genetic differentiation as a function of distance.

Fig. 4.5 Galapagos penguin (*Spheniscus mendiculus*) at Sullivan Bay, Santiago Island. Photo by Ben Nims

4.3 Diversity at Genes Under Selection—Major Histocompatibility Complex

Heterozygosity at neutral loci is often used as a proxy for variability at functional genes when investigating fitness correlations; however, assessing variability at loci directly involved in immune function may be more instructive. Associations between genetic polymorphisms and susceptibility to particular diseases have been demonstrated for a variety of immune loci (reviewed in Acevedo-Whitehouse and Cunningham 2006). The greatest amount of effort has focused on genes of the major histocompatibility complex (MHC). MHC molecules bind to peptides derived from intracellular (MHC class I) and extracellular (class II) pathogens and present them to T cells, thus initiating the adaptive immune response (Janeway et al. 2001). Due to their function, MHC genes typically have high levels of polymorphism at the exons coding for the peptide-binding regions. This variation is maintained through balancing selection, likely driven by parasite-mediated natural selection and MHC-dependent sexual selection (reviewed in Garrigan and Hedrick 2003; Piertney and Oliver 2006; Spurgin and Richardson 2010).

4.3.1 MHC Diversity in Small, Bottlenecked Populations

As a result of selection, MHC genes in large, outbred populations typically have large numbers of alleles and high nucleotide diversity between alleles (Westerdahl et al. 2004; Promerová et al. 2009). However, MHC genes are also subject to founder events and genetic drift, which may overwhelm the effect of balancing selection (Maruyama and Nei 1981; Kimura 1983). In a review of natural populations, Radwan et al. (2010) found much evidence for reduced MHC variability in bottlenecked or island populations due to drift. Bottlenecked mainland populations may exhibit extremely low MHC variability. For example, six Eurasian beaver populations were each monomorphic for a different allele at the DRB region sequenced (Babik et al. 2005). In a bottlenecked population of Greater prairie-chickens (*Tympanuchus cupido),* a contemporary population sample possessed 33% fewer class II alleles than an historic sample (Eimes et al. 2011). Similarly, island populations often exhibit reduced MHC diversity (Seddon and Baverstock 1999; Miller and Lambert 2004). Richardson and Westerdahl (2003) recovered only 10 class I sequences from the endemic Seychelles warbler (*Acrocephalus sechellensis*), which has also experienced a bottleneck, whereas they found 67 sequences in the Great reed warbler (*A. arundinaceus*), a mainland congener.

Nevertheless, several examples exist of populations that have lost neutral variation due to drift but have retained relatively high MHC variation. A small, upstream guppy population was genetically distinct from and had reduced neutral variation compared to a larger, downstream population (van Oosterhout et al. 2006). However, the two populations had similar levels of allelic richness at MHC loci, with no differentiation, a pattern the authors attributed to selection. A recent study comparing six mainland and six island populations of house sparrows showed that microsatellite diversity was lower within the island populations, while MHC diversity was similar between island and mainland populations, possibly a result of selection (Bichet et al. 2015).

4.3.2 Examples from Galápagos

MHC diversity has been investigated in a few species endemic to the Galápagos Islands. Bollmer et al. (2011) described class II exon 2 variability in 32 Galápagos hawks (representing all 8 extant populations) and 20 Swainson's hawks. The primers appeared to amplify two loci (they recovered 2–4 sequences per individual), and the sequences clustered into two distinct groups in a phylogenetic network, one of which (Group 1) had lower nucleotide diversity than the other (Group 2). Three different sequences were recovered from the 32 Galápagos hawks: one was present in all individuals (Buga*01, possibly a fixed Group 1 locus), while all individuals had one or both of the other two sequences, Buga*02 and Buga*03, which clustered into Group 2. These latter two sequences differed from each other by only 1 bp (a nonsynonymous mutation), but they differed from Buga*01 by 30 and 31 bp, respectively, out of the 255 bp analyzed. In contrast, the 20 Swainson's hawks exhibited a greater number of sequences (19 overall) with higher nucleotide diversity than those of the Galápagos hawk (Table 4.2).

Similarly, the Galápagos penguin exhibits reduced MHC diversity compared to its closest relatives. Bollmer et al. (2007) amplified a portion (157 bp) of class II exon 2 from a single locus (penguins species are thought to have only one class II locus; Kikkawa et al. 2009) in 30 individuals from 8 breeding colonies encompassing the species range in Galápagos. The penguins possessed three different sequences differing by only 1–3 bp. MHC diversity has also been characterized for two congeners: the Humboldt penguin (*S. humboldti*; Kikkawa et al. 2005) and the Magellanic penguin (*S. magellanicus*; Knafler et al. 2012). The 20 Humboldt penguins (15 of which were from a captive population) did not have many more alleles (6 vs. 3 in Galápagos penguins), but their sequences were more divergent, with more polymorphic sites (Table 4.2). A natural population of Magellanic penguins exhibited much more diversity, having 28 alleles in 100 individuals, with 31 polymorphic sites at the same 157 bp (Table 4.2).

The pattern of low MHC diversity in the Galápagos endemics compared to their closest mainland relatives mirrors the pattern found at neutral loci. This strongly suggests that a genetic bottleneck upon foundation and/or continued drift in small populations have greatly impacted MHC diversity. Both the Galápagos hawk and penguin have few sequences, and the sequences differ by only a few polymorphic sites. The high similarity of the alleles suggests that these loci became fixed, and then new alleles arose through point mutation after colonization of Galápagos. It is possible that very similar alleles were retained from their ancestral populations and divergent alleles were lost, but this seems unlikely. In other species experiencing similar bottlenecks, divergent alleles were retained (Hedrick et al. 2000; Lau et al. 2014). In the Seychelles warbler, sequences were just as divergent as those present in mainland populations, though fewer in number (Richardson and Westerdahl 2003).

Reduced MHC diversity in island species compared to their mainland relatives could also be due to ecological factors influencing selective pressure. Due to their isolation, island populations may experience weaker pathogen pressure than mainland populations (Fromont et al. 2001; Beadell et al. 2007), which could result in relaxed selection pressure to maintain MHC diversity (Slade 1992; Westerdahl et al. 2004). Swainson's hawks migrate between their breeding ground in North America and their wintering ground in Argentina, whereas Galápagos hawks are much more sedentary, exhibiting little to no gene flow among islands (Bollmer et al. 2005, 2006; Koop et al. 2014). Swainson's hawks, on their long migrations, are exposed to a much greater diversity of parasites than are Galápagos hawks. For example, Galápagos hawks carry three co-evolved louse species (Whiteman et al. 2006), compared to five for Swainson's hawks (Price et al. 2003).

It might be expected that Galápagos penguins would be under stronger selection by pathogens than other penguin species given their tropical locality. However, the isolation of Galápagos could still keep pathogen exposure to a minimum. In a health survey, Galápagos penguins were found to be seronegative for 14 common avian viruses (Travis et al. 2006). Of greatest concern is the discovery of *Plasmodium*

Table 4.2 MHC diversity in two Galápagos endemics compared to their closest relatives. The number of samples (N), base pairs of MHC class II exon 2 analyzed, alleles (A), polymorphic sites (P), p-distances, and nucleotide diversity are given

Species	N	Bp of exon 2	A	P	p-distance (+SE)	Π
Galápagos hawk (group 1)[a]	32	255	1	n/a	n/a	n/a
Swainson's hawk (group 1)[a]	20	255	9	16	0.024 ± 0.006	0.018
Galápagos hawk (group 2)[a]	32	255	2	1	0.004 ± 0.004	0.002
Swainson's hawk (group 2)[a]	20	255	10	53	0.090 ± 0.012	0.080
Galápagos penguin[b]	30	157	3	3	0.013 ± 0.007	0.008
Humboldt penguin[c]	20	157	6	20	0.062 ± 0.013	0.040
Magellanic penguin[d]	100	157	28	31	0.068 ± 0.012	0.061

N number of individuals, *Bp* Base pairs, *A* number of alleles, *P* number of polymorphic sites, π nucleotide diversity

[a] Data from Bollmer et al. (2011); p-distances and nucleotide diversity calculated from JL Bollmer and PG Parker (unpublished genotypic data) using MEGA v7 (Kumar et al. 2016)

[b] Data from Bollmer et al. (2007); p-distances and nucleotide diversity calculated from JL Bollmer and PG Parker (unpublished genotypic data) using MEGA v7 (Kumar et al. 2016)

[c] Data calculated from Kikkawa et al. (2009) using MEGA v7 (Kumar et al. 2016)

[d] Knafler et al. (2012)

infecting the penguins (Levin et al. 2009, 2013). Palmer et al. (2013) detected a high seroprevalence (97.2%) of anti-*Plasmodium* spp. antibodies, suggesting that exposure to avian malaria is widespread among the penguins. However, it appears that the parasite is not completing its life cycle in the penguins as evidenced by the lack of gametocytes in blood smears, and data indicate that the penguins are able to survive infection (Palmer et al. 2013).

Alternatively, instead of relaxed selection pressure, the presence of a few, very similar MHC sequences could be due to a selective sweep for a certain advantageous MHC profile (de Groot et al. 2008). This seems improbable in the Galápagos hawk as health surveys have not identified a candidate parasite that is likely to exert such strong selective pressure (Deem et al. 2012), unless one occurred in the past. In the Galápagos penguin, on the other hand, it is possible that the MHC sequences present are effective at combating the *Plasmodium* strains present in Galápagos. Studies in other bird species have identified correlations between specific MHC alleles and an individual's susceptibility to avian malaria (Bonneaud et al. 2006; Jones et al. 2015). While reduced selection pressure or a selective sweep cannot be ruled out as explanations for the low MHC variability in the Galápagos hawk and penguin, these would not explain the corresponding loss of variability at neutral loci. Thus, genetic drift due to founder events and small population size is the most likely explanation.

Class II MHC variation has also been investigated in Galápagos mockingbirds (Fig. 4.6). Vlček et al. (2016) genotyped 177 mockingbirds from 12 Galápagos islands, as well as 12 continental mockingbirds (*Mimus polyglottos*), at a 164 bp class IIB exon 2 fragment. The mockingbirds exhibited much higher MHC variability than the hawks and penguins; the number of alleles per individual ranged from 1 to 12, and the number of alleles per Galápagos mockingbird population ranged from

13 to 48. Amino acid distances between alleles were higher than those in the hawks and penguins, with amino acid sequences differing by an average of 18% within individuals. At the population level, both number of MHC alleles (R^2-adj = 0.346, $P = 0.026$) and microsatellite allelic richness (R^2-adj = 0.572, $P = 0.003$) were significantly correlated with island area; furthermore, the effect of island size was similar for both markers as the slopes did not differ. The number of MHC alleles per individual, however, was not related to island size.

Comparisons with the mainland population showed varying patterns. Neutral microsatellite diversity was significantly lower in Galápagos populations compared to *M. polyglottos* (allelic richness of 2.7 and 5.8, respectively; average heterozygosity of 0.396 and 0.651, respectively), consistent with the effects of drift. In contrast, the number of MHC alleles per population was similar between Galápagos mockingbirds (mean of 25, range of 13–48) and the number of alleles within *M. polyglottos* ($N = 32$). The number of MHC alleles per individual was also similar between island and mainland samples; however, the average intra-individual amino acid distance in *M. polyglottos* was twice that in Galápagos populations (except for one outlier, Santa Fe).

While the Galápagos hawks and penguins exhibited clear reductions in diversity at both neutral and MHC loci, indicating a strong influence of genetic drift, patterns within Galápagos mockingbirds provide some evidence for selection. Vlček et al (2016) noted population allelic diversity was correlated with island area (consistent with drift), but intra-individual allelic diversity and amino acid distance were not. Furthermore, Galápagos mockingbirds exhibited high levels of allele sharing across populations, despite strong neutral structuring. The authors suggested that selection has acted to maintain some ancestral MHC diversity, but noted that more attention should be paid to how various measures of diversity (e.g., amino acid distance, intra-individual alleles, population allelic diversity) may be affected differently by evolutionary forces. This was further demonstrated in the island-mainland comparison, where number of MHC alleles (intra-individual and population-level) was similar, but intra-individual amino acid distance was higher on the mainland. Vlček et al. hypothesized selection has maintained an optimal number of MHC alleles in Galápagos and on the continent, but that neutral forces may be more responsible for the difference in amino acid distances.

4.4 Genetic Variation and Fitness Correlates

Some studies have taken analysis of genetic variability a step further by investigating how it may affect different aspects of fitness. The relative ease of measuring variability at neutral loci has resulted in a large literature examining heterozygosity-fitness correlations (HFCs). Neutral marker heterozygosity may potentially be representative of genome-wide or functional heterozygosity if the neutral loci are in

Fig. 4.6 Floreana mockingbird (*Mimus trifasciatus*). This species occurs today only on Gardner and Champion, two islets off the coast of Floreana. Photo: Paquita Hoeck

linkage disequilibrium with fitness loci, or if they are in identity disequilibrium, where there is a fitness cost of homozygosity (reviewed in Chapman et al. 2009). In general, HFCs are weak (Chapman et al. 2009); nevertheless, studies have found relationships between microsatellite heterozygosity and fitness measures, such as morphological traits, behavior, survival, reproductive success, and immune response (e.g., Olano-Marin et al. 2011; Forstmeier et al. 2012).

At genes directly involved in disease resistance, patterns are similarly complicated. Studies of parasite-mediated selection on the MHC have found evidence for heterozygote advantage (Osborne et al. 2015), divergent allele advantage (Lenz et al. 2013), an intermediate number of alleles being optimal (Kalbe et al. 2009), specific alleles conferring increased resistance or susceptibility (Bonneaud et al. 2006; Jones et al. 2015), or a combination of these patterns (Eizaguirre et al. 2012; Sin et al. 2014). These same patterns are seen with other fitness-related measures that may be indirectly related to pathogen pressure, such as survival, reproductive success, and advantageous morphological traits (e.g., Dunn et al. 2013). Interestingly, patterns of heterozygote advantage at MHC loci may not be mirrored by genome-wide heterozygosity as measured by microsatellite loci (Worley et al. 2010; Osborne et al. 2015).

Studies do not always find relationships between genetic markers and measures of fitness (Chapman et al. 2009). Interactions are complex and the ability to detect patterns is dependent on many factors, such as the genetic markers chosen, sample size, the fitness components measured, the number and type of pathogens characterized, and strength of selection.

4.4.1 Examples from Galápagos—Immune Function and Parasite Resistance

The relationship between genetic variation and immune function has been investigated in several Galápagos species. Whiteman et al. (2006) assessed natural antibody (NAb) titers in Galápagos and Swainson's hawks. NAbs are nonspecific antibodies that prime the adaptive immune response, and their levels may be an indicator of adaptive antibody levels (Adelman et al. 2004; Parmentier et al. 2004). Using multilocus minisatellite heterozygosity as a proxy for genome-wide heterozygosity, Whiteman et al. (2006) showed that Swainson's hawks on average were more heterozygous with higher NAb agglutination titers and lower average louse abundance than the more inbred Galápagos hawk populations (Fig. 4.7). Among Galápagos hawk populations only, louse abundance was negatively correlated with genetic diversity (Fig. 4.7a). The relationship between NAb titers and heterozygosity was less straightforward. Whiteman et al. found a significant effect of island on NAb titers, but it was nonlinear, with the more outbred populations having intermediate titers, while the two most inbred had low titers and a third inbred population had the highest average titer (Fig. 4.7b). The variance was lower within inbred populations than outbred ones. At the individual level, body louse abundance was weakly negatively correlated with NAb titer after controlling for the effects of island in a GLM.

In contrast to the above, Hoeck and Keller (2012) did not detect a relationship among inbreeding, innate immune function, and ectoparasite load in an extensive study of Galápagos mockingbirds. The authors sampled mockingbirds from 13 sites on 11 islands, and they acquired data for four response variables: (1) genotypes at 26 microsatellite loci to calculate measures of genetic variability and inbreeding; (2) the ratio of heterophils to lymphocytes in the blood, a measure of stress (Davis et al. 2008); (3) agglutination and lysis titers, measures of strength of immune response, following Matson et al. (2005); and (4) louse load. Measures of inbreeding were not correlated with any of the other three response variables. Lysis and number of feather lice were positively correlated, but only at the population level ($r^2 = 0.36$, $p = 0.023$). The overall lack of a relationship among these response variables is somewhat puzzling, but Hoeck and Keller offered several possible explanations: inbreeding may not affect the innate immune traits and ectoparasite species studied, tradeoffs between different measures of immunity could obscure any relationships, deleterious alleles may already have been purged, pathogen pressure may not be strong enough for inbreeding to have a detectable effect on the immune variables measured, or a lack of statistical power prevented them from detecting associations.

In addition to these avian studies, the relationship between heterozygosity and immune function has also been investigated in the Galápagos sea lion. Brock et al. (2015) sampled two age groups (pups and juveniles) from two different islands: a control colony on uninhabited Santa Fe and a human-impacted colony in a town on San Cristóbal. They measured IgG concentration and total leukocyte concentration, and they genotyped individuals at 23 microsatellite loci in order to calculate homozygosity weighted by locus (HL). In the control colony, relatively heterozygous

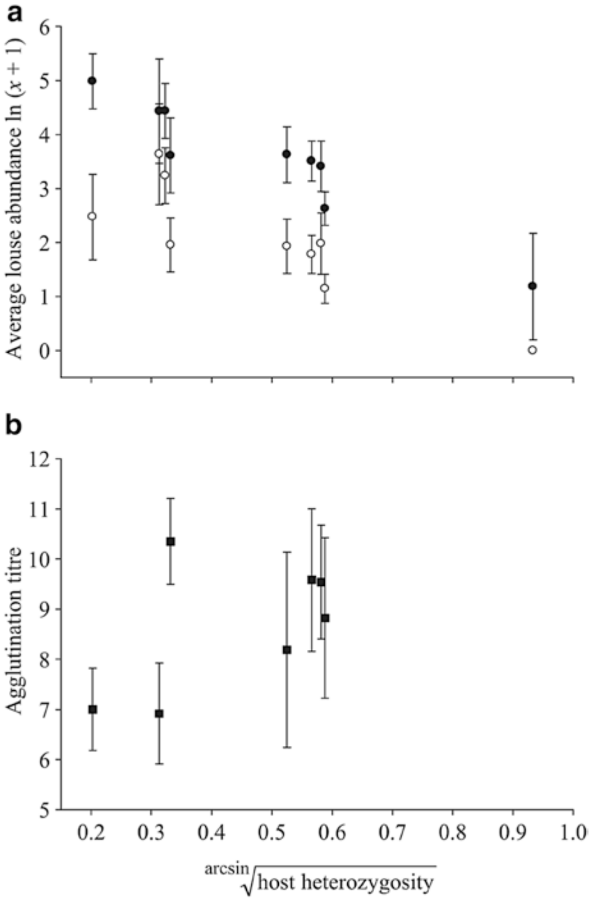

Fig. 4.7 (**a**) Average amblyceran (*closed circle* with ±95% confidence intervals) and ischnoceran (*open circle*) louse abundance versus host population genetic diversity, (**b**) Average natural antibody agglutination titers (±SD) versus host population genetic diversity (Reproduced from Whiteman et al. (2006))

pups had shorter body lengths, but they produced higher levels of IgG. This pattern was not present in the San Cristóbal colony; the authors speculated that this could be because San Cristóbal pups varied less in heterozygosity, and pups in that colony had higher IgG levels, both of which could obscure a relationship between genotype and IgG production. Total leukocyte concentration was not statistically related to HL in either colony; however, there was a trend of increased leukocyte concentration in homozygous juveniles in the human-impacted colony, possibly due to increased pathogen exposure and/or susceptibility. These results must be viewed with the caveats that it is a correlative study and only one human-impacted colony and one uninhabited island were sampled. However, this work hints at the importance of considering environmental context when investigating relationships between heterozygosity and immune function.

4.4.2 *Examples from Galápagos—Survival and Reproductive Success*

In a study of two finch species, the medium ground finch (*Geospiza fortis*) and cactus finch (*G. scandens*), on Daphne Major, Markert et al. (2004) were able to compare inbreeding as measured by pedigree and genetic diversity calculated from 13 microsatellite markers in relation to fitness. All individuals included in the study were from the same brood year to control for environmental effects. *Geospiza fortis* individuals that recruited into the breeding population had higher heterozygosity than nonrecruits, and lifespan was positively correlated with heterozygosity. This pattern was absent for *G. scandens*, possibly due to the smaller sample size. Pedigree-based inbreeding coefficients were significantly higher in nonrecruits than recruits for both *G. fortis* and *G. scandens*.

The waved albatross, *Phoebastria irrorata*, nests on only one island (Española) in Galápagos, and individuals are known to engage in extra-pair copulations resulting in offspring sired by males other than the social father at the nest (Huyvaert et al. 2000). Using multilocus minisatellites, Huyvaert and Parker (2010) found that social parents with higher genetic similarity were more likely to have an egg that did not hatch, possibly a cost of inbreeding.

The effect of genotype on reproductive success has also been investigated in the Galápagos sea lion. Lenz et al. (2013) evaluated genetic diversity of males, females, and pups at an MHC-DRB gene and 22 microsatellite loci. Offspring body condition at birth was significantly positively associated with the degree of divergence between the two maternal MHC alleles (but not the offspring's own genotype) based on amino acid differences, although this effect was no longer measurable at 1 year of age. Offspring were significantly more likely to survive to reproductive age if their own MHC alleles were divergent or if their mothers' alleles were divergent. Microsatellite-based estimates of inbreeding (which were low overall) were not correlated with offspring survival, nor were particular MHC alleles. Female reproductive success was also related to the female's MHC genotype; females having a larger number of surviving offspring had a greater or optimal level of amino acid divergence between their two alleles.

4.5 Low Genetic Variability: Conservation Implications in a Changing World

We have established that a number of the bird species in Galápagos are genetically depauperate at both neutral and functional loci. What are the implications of this? Bottlenecked populations are known to be vulnerable to inbreeding depression, which may negatively impact individual fitness (Keller and Waller 2002) and make populations more susceptible to extinction (Reed and Frankham 2003). On the other hand, some bottlenecked populations subsequently have rebounded and undergone expansions, despite having lost much genetic variability, including at MHC genes (Mikko and Andersson 1995; Babik et al. 2005, 2009).

The greatest threat to the endemic birds of Galápagos is likely the introduction of a novel disease (Wikelski et al. 2004; Parker et al. 2006; Eastwood et al. 2014). The dramatic decline and extinction of Hawaiian honeycreepers following the spread of avipoxvirus and *Plasmodium* is a stark example of the danger posed by pathogens introduced to immunologically naive island birds (Warner 1968; Atkinson et al. 2000). Inbreeding and low genetic variation have been shown to be associated with increased susceptibility to pathogens in a number of wild populations (Acevedo-Whitehouse et al. 2003; Townsend et al. 2010).

Understanding the allelic repertoire a species possesses can be critical to making impactful management decisions. For example, the emerging chytrid fungal disease has caused dramatic population declines and extinctions in amphibians (Fisher et al. 2009). However, Bataille et al. (2015) have experimentally demonstrated a link between particular MHC class II amino acid motifs and resistance to this fungal infection in a tree frog. Also, studies in sparrow species have found evidence for correlations between susceptibility to hemosporidian infection and particular MHC alleles (Bonneaud et al. 2006; Loiseau et al. 2008; Jones et al. 2015). Similar information might prove useful should an emergent disease strike Galápagos species. Alternatively, instead of targeting specific alleles, attempting to increase fitness through genome-wide outcrossing may be effective. In a recent meta-analysis studying the fitness effects of gene flow into inbred populations, Frankham (2015) found that the effects were beneficial in the vast majority of cases. Outcrossing resulted in a 148% higher composite fitness under stressful environmental conditions. This clear pattern led Frankham to advocate that managers make better use of gene flow to genetically rescue inbred populations and provide them with increased evolutionary potential. This may not be desirable in a setting such as Galápagos where retaining species in their most natural evolutionary state is a high priority, but it might still be considered when a population becomes critically small.

Study of native Galápagos species has made an unparalleled contribution to our understanding of evolutionary processes, and through continued research into the population genetics of these species, we will better understand disease dynamics on islands and make more informed conservation decisions to protect this unique place.

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Chapter 5

From the Vagile to the Sedentary: Disease Implications and New Host Relationships on Islands

David Cameron Duffy and F. Hernan Vargas

Abstract How species come to be established on islands and their consequent adaptations and evolution are subjects that lie at the heart of much of ecology and evolutionary and conservation biology. On islands, small populations, limited gene diversity and flow, and simpler ecosystems facilitate our understanding of how species arrive and then adapt and evolve in new locations. One component of this is understanding how the transition from arrival to establishment may affect species and their parasites and diseases. Colonizing species may arrive without the full burdens of parasites weighing on their source populations, allowing them to reduce their energetic investments in immune defenses. However, reduced genetic diversity may also reduce populations through inbreeding depression or diminish capacity to evolve. Loss of genes and adaptation to novel environments may over time reduce the capacity of insular species to deal with new parasites or old ones that "catch up." With increasing anthropogenic introduction of novel biotas, including parasites, to islands, the conservation of insular biodiversity becomes increasingly challenging, which in turn reduces our ability to study and understand both islands and diseases.

Keywords Arrival • Establishment • Parasites • Flightlessness • Adaptive radiation • Extinction

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5.1 Introduction

Islands have been the anvil upon which much of our theoretical understanding of evolution and ecology has been hammered out. They have a similar promise for our understanding of diseases, especially emerging ones.

Did species arrive on islands over past or present land bridges (Hooker 1844; Gregory 1928)? Did they follow successive island "stepping stones" generated over "hot spots" or islands exposed by changes in sea level (Simpson 1940; Wagner and Funk 1995; Gillespie and Roderick 2002; Parent et al. 2008)? Or did they arrive through the lottery of long-distance dispersal (Darwin 1860)? The theories of island biogeography (MacArthur and Wilson 1967; Whittaker et al. 2008), taxon cycles (Wilson 1961; Ricklefs and Bermingham 2002) and Darwin's naturalization hypothesis that new species most dissimilar to those already present are most likely to be successful (Darwin 1860; Elton 1958; Daehler 2001) have been used to explain arrival, establishment, and subsequent fates of species. The theories of assembly rules and unified neutral theory of biodiversity and biogeography provide contrasting views of how subsequent communities are organized: the former, deterministic; the latter, random (Diamond 1975; Hubbell 2001; Götzenberger et al. 2011). The metapopulation theory of island habitats has focused on the behavior and persistence of species populations across discontinuous island-like landscapes (Hanski and Gaggiotti 2004). Island theory has also helped shape the design and management of natural areas to protect diversity (Simberloff and Abele 1976, 1982). More recently, understanding the establishment and ecological impacts of alien invasive species has also focused on islands, whether true islands or habitat remnants, both for conservation and to provide insights into continental systems (e.g., Mack et al. 2000).

Islands have given us a wealth of examples of evolution and the adaptive radiation of founder species (Darwin 1839; Carlquist 1965; Schluter 2000; Carlquist et al. 2003; Grant and Grant 2014) that laid the foundation and furthered the development of one of the central theories of biological science, evolution through natural selection (Darwin 1860; Wallace 1870).

This chapter provides an overview of how arriving and becoming established and sedentary on islands interact with the population biology and parasite ecology of island species. What makes a species a good colonizer may make it unsuitable for longer-term persistence on an island. On the other hand, adapting to an island and becoming sedentary may make species vulnerable to novel changes in their environment, including the arrival of new parasites and diseases. Other chapters focus more specifically on the ecology and evolution of disease in Galapagos.

Our focus is on terrestrial species on Pacific oceanic islands, those beyond continental shelves that have never been connected to the mainland. Colonization of these islands is different from that of islands closer to species sources and the challenges of establishment and persistence may be different.

The topics covered here have generated an extensive, distinguished, and often contentious literature. This chapter can at best serve as a modest introduction to the various lines of thought and research. We have tried to combine both the "classic" literature and newer papers to reflect the diversity of approaches, subjects, and geographic areas. The chapter is divided into three main units: how species get to islands, the consequences of becoming established on islands, and the subsequent effect of disease.

5.2 Getting There

Islands are not static in geological time. The geodynamics of islands affect how species reach islands and which species persist and diversify over time (Darwin 1860; Lim and Marshall 2017). Islands may rise from the ocean as volcanoes over "hot spots." They may disappear as their own weight, erosion, landslides, or changes in sea level sink them or link them to continents (e.g., Darwin 1842). New and old islands may be smaller and lower with fewer habitats and geographic discontinuities, while "middle aged" islands may be high, with variations in topography, climate, and environments (e.g., Whittaker et al. 2008) (Fig. 5.1) leading to changes in colonization, speciation, and extinction (Fig. 5.2). Changes in sea level, atmospheric circulation, and ocean currents may also affect accessibility of islands (Ali and Huber 2010; Claridge et al. 2017).

For islands close to continents, colonization may be by rafting or by dispersal across a land bridge during periods of lower sea level or by being stranded with a rising sea level (Matthew 1918; Simpson 1940). For oceanic islands, successful settlement may be by successive moves down a chain of past or present islands, by "sweepstakes" long-distance dispersal, landing in a suitable spot in a sea of hostile habitats, or by repeated colonizations of islands within an archipelago

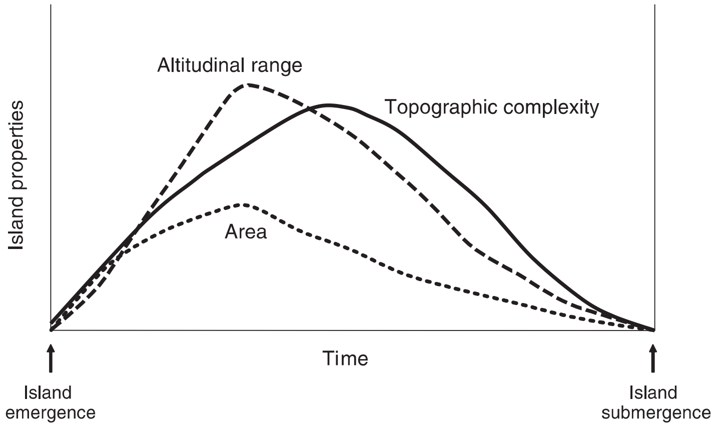

Fig. 5.1 Simplified oceanic island geodynamics over time. Altitude and area accumulate over time, followed by topographic complexity, then all diminish with erosion, land slides and subsidence (Figure 3 from Whittaker et al. 2008)

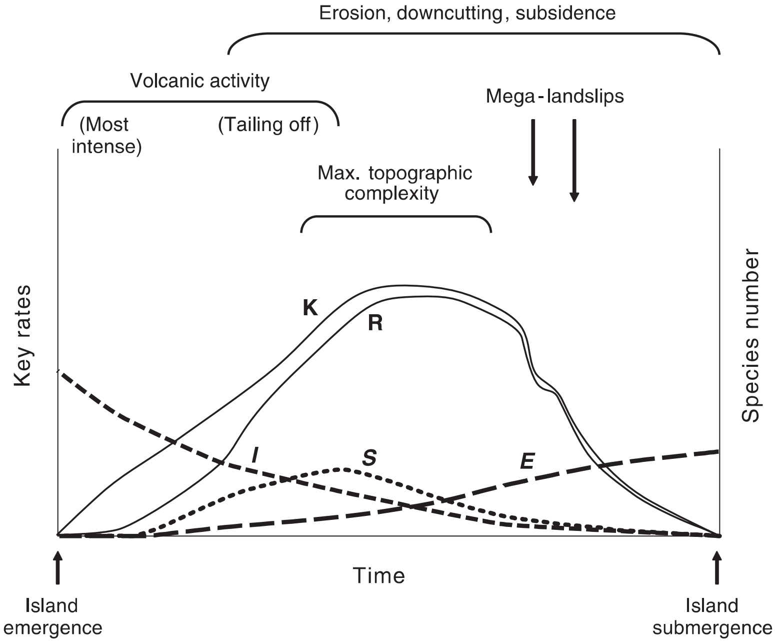

Fig. 5.2 Idealized model of biological change and oceanic island dynamics. *I* is immigration rate, *S* is speciation rate, *E* is extinction rate, *K* is the carrying capacity, and *R* is the number of species. Species and speciation increase after the island rises from the sea because of volcanic activity. As the island reaches a plateau in topographic complexity volcanism diminishes, and *K* and *R* reach their maxima, with *I* declining. As erosion and landslides eventually reduce the island to sea level, *K* and *R* decrease and *E* rises (Figure 4 from Whittaker et al. 2008)

(Fig. 5.3) (Darwin 1860; Simpson 1940; Wagner and Funk 1995; Shaw and Gillespie 2016).

Colonizing species of oceanic islands tend to have characteristics often identified in the literature with "invasive species," "supertramps," and weediness that predispose them to vagrancy and establishment. Characteristics include small size, wide habitat tolerances, high fecundity, early age of reproduction, and a willingness and ability to cross water gaps (Carlquist 1966a; Diamond 1974). For plants, good dispersers tend to be self-fertilizing with propagules that are small or have winglets and are wind-dispersed, with barbs and fruits that attach to or pass through birds, or float for water dispersal (Carr 1987; Aoyama et al. 2012), a range that can be described as taking advantage of "wind, waves, wings." In addition, for anything from seeds to medium-sized animals, rafting may transport flightless species to isolated islands (Simpson 1940; Claridge et al. 2017). Even the most improbable species undertake unlikely dispersals (Hansen et al. 2016), such as the recent record of an Aldabra giant tortoise *Dipsochelys dussumieri* that reached the African mainland almost 750 km away (Gerlach et al. 2006). Table 5.1 shows the estimated contributions of wind, sea, and birds to the arrival of different components of the Hawaiian biota. Arrivals are not frequent and vary between taxa. Ziegler (2002) estimated the

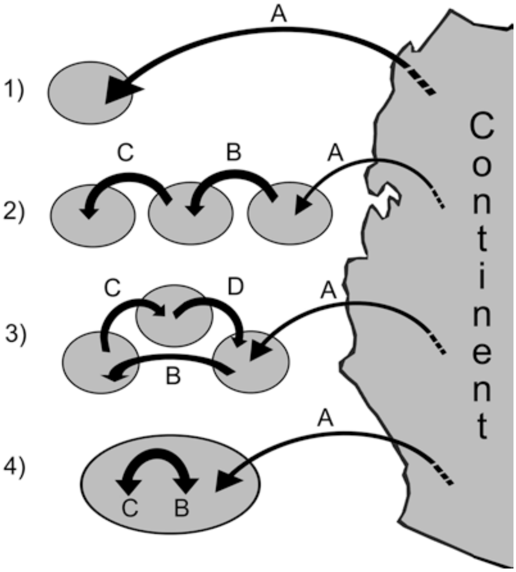

Fig. 5.3 Different types of colonization and speciation on islands. (*1*) "Jackpot" dispersal to an isolated island. (*2*) "Stepping stone" colonization and speciation down an island chain, (*3*) Colonization of an archipelago and subsequent allopatric speciation within the archipelago, (*4*) Colonization of a single island and consequent allopatric speciation within the island

Table 5.1 The estimated percentage importance of various means of transport for species reaching the Hawaiian Islands (after Ziegler 2002)

Group	Sea	Wind	Birds
Ferns		95	5
Flowering plants	23	2	75
Insects	**	***	*
Spiders	**	***	*
Snails	**	*	***
Fishes	100		
Birds		100	
Mammals		100	

*** = most important, ** = important, * = least important

average interval between arrival of founding species of different taxa, ranging from 70K years for insects to 15M years for mammals (Table 5.2).

Not all species get to oceanic islands, so the resulting biota is termed "disharmonic" in that whole groups are rare or absent or over-represented compared to the mainland, depending on their dispersal ability (Carlquist 1966a). Species that fail to become established may have factors that limit them, such as requiring forests or freshwater habitats or specific pollinators or dispersers. Parasites typically need to be transported by their hosts, unless the parasite has catholic tastes or can switch to other hosts upon arrival (Solarz and Najberek 2017; Blackburn and Ewen 2016).

Table 5.2 The estimated average number of years (1000×) between arrivals of successful founding species in Hawaii (after Ziegler 2002)

Marine	
Seaweed	175
Stony Coral	1800
Molluscs	115
Inshore Fish	175
Terrestrial	
Ferns and Allies	265
Flowering Plants	105
Insects	70
Siders	2310
Snails	1035
Freshwater Fish	6000
Birds	1155
Mammals	15,000

5.3 Being There

5.3.1 *Becoming Sedentary*

There are various definitions of being sedentary. At one extreme are plant and marine invertebrate species that are sessile, fixed in one spot, dispersing only through seeds or larval stages. At the other extreme are ruderal or pioneer plants and animals that live in unstable environments and are dependent on dispersal to find new suitable habitats as the old ones become unsuitable (Shelford 1914). If there is only limited colonization, there may be a lower probability that the full complement of a species' baggage of predators, parasites, and diseases will accompany it, leading to predator or parasite "release" (Liu and Stiling 2006), although the effects are neither universal nor clear cut (Colautti et al. 2004; Lester et al. 2015).

Adaptation to an island, decreased gene flow, and an increase in sedentariness can have genetic, physiological, morphological, behavioral, ecological, and evolutionary consequences. These are considered below.

5.3.1.1 Genetic

The smaller or more distant the island from a source, the greater the selection for a species to become sedentary once it colonizes. Further dispersal beyond the island would have a reduced probability of survival. The more distant the island, the lower the probability of gene flow from outside and the greater the probability that only a reduced genetic diversity reaches the island, producing a "founder effect" (Templeton 1980). The smaller the island, the smaller the sustainable carrying capacity "K" for a population and the greater the probability that genetic diversity will become reduced over time with less chance of mutations that might facilitate selection for adaptation to the new environment. Inbreeding and genetic drift in such small populations may also allow the accumulation of lethal and other deleterious genes that may reduce population viability (e.g., Kennedy et al. 2014). Frankham (1997) reported lower genetic diversity for island endemics than for nonendemic birds and mammals. García-Verdugo et al. (2015) reported that while neutral genetic diversity in plants did not differ between island and mainland populations, island endemics with narrow distributions did have lower genetic diversity. While the genetics of colonization would seem likely to set the stage for decreasing dispersal, movement, and survival in new populations, on the other hand, they could produce rapid adaption and novel responses to the new environment (Darwin 1860).

5.3.1.2 Morphological

Among the most famous adaptive responses of organisms to islands are extreme changes in morphology in endemic species (Carlquist 1965). Changes may include gigantism, producing the giant tortoises of Galapagos and Aldabra (Geotestudinae), elephant birds and rodents of several hundred kilograms (Biknevicius et al. 1993; Murray and Vickers-Rich 2004), dwarfism such as in deer, elephants, and humans (Lister 1996; Brown et al. 2004). Such changes are not universal and the causes of such extremes may be complex and phylogenetically or climatically constrained, suggesting caution in generalization (Lomolino 2005; Meiri et al. 2008; van den Hoek Ostende et al. 2016).

There may also be changes in body proportions and sexual dimorphism (Losos et al. 2003; Wright et al. 2016). Flightlessness has evolved repeatedly in island birds, such as rails (Rallidae) across the Pacific (Ripley and Lansdowne 1977), kiwis (*Apteryx* spp.) in New Zealand, the Flightless Cormorant (*Phalacrocorax harrisi*) in Galapagos (e.g., Slikas et al. 2002; Burga et al. 2017) and geese (*Branta* spp.) and ducks (*Thambetochen* spp.) in Hawaii (Sorenson et al. 1999). Wright et al. (2016) found that volant island birds tend toward reduced flight muscle mass and longer legs, reducing the potential for dispersal. Island beetles also tend to flightlessness (Darwin 1860, Zimmerman 2017) and Carlquist (1966b, c) noted reduced dispersal in the Hawaiian flora.

Reduction or loss of flight may reduce energetic requirements. In New Zealand the lesser short-tailed bat (*Mystacina tuberculata*) walks and even burrows through substrate, expanding its diet and reducing energetic demands while foraging (Hand et al. 2009). Flightlessness in extinct Hawaiian birds may have allowed them to exploit lower value food such as ferns as important, if not primary, dietary items (James and Burney 1997). The flightless New Zealand Takahe (*Notornis mantetli*) feeds on fern rhizomes in winter (Mills et al. 1980).

Species can also evolve to exploit "empty niches," as suggested here for Hawaiian bird species (Fig. 5.4). Filling the "woodpecker niche," extracting insects from below the bark of trees, the woodpecker finch (*Camarhynchus pallidus*) in Galapagos uses thorns to probe crevices in bark for insects. In Hawaii, Maui Parrotbills (*Pseudonestor xanthophrys*) have "can opener" bills to pry open bark. The now

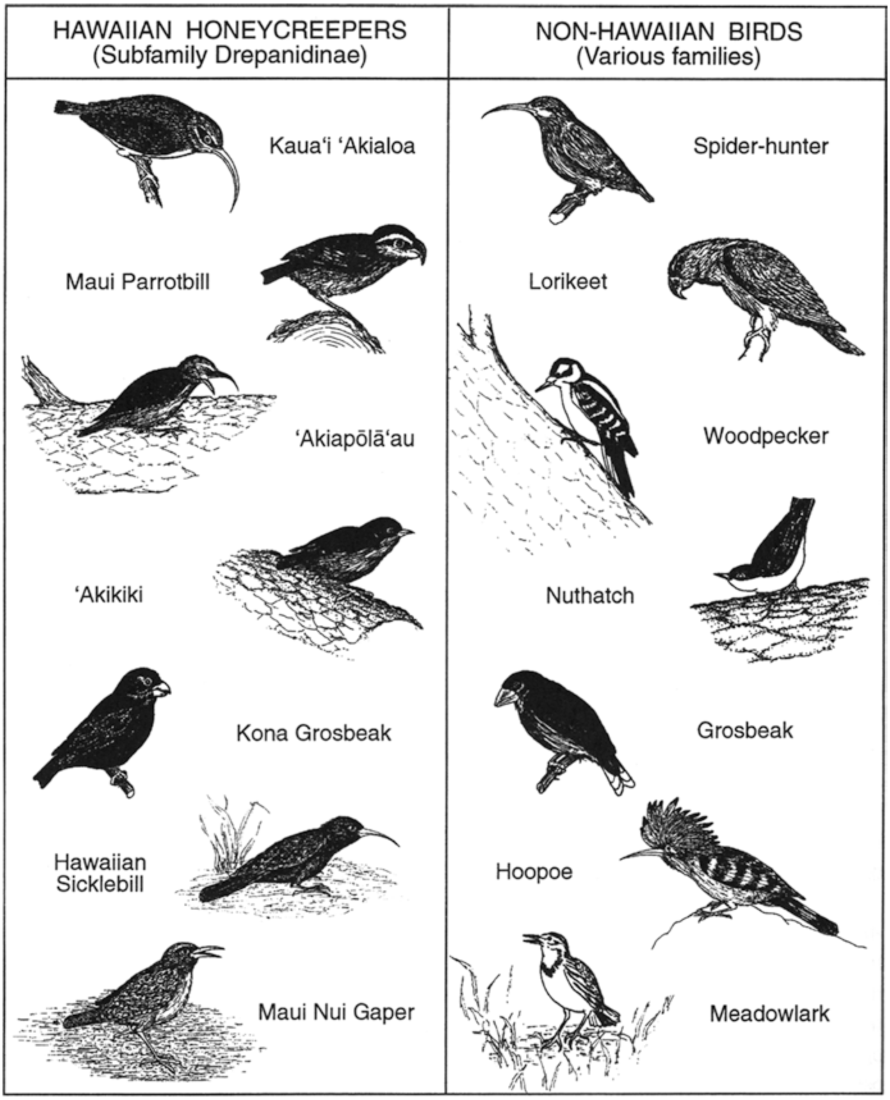

Fig. 5.4 Convergence of Hawaiian honeycreepers to occupy various "empty niches" or ecotypes found in birds elsewhere (reproduced from Ziegler 2002, Figure 10.4, with permission of the University of Hawaii Press)

extinct Hawaiian nukupu‘u (*Hemignathus lucidus*) had a lower mandible used as a wedge and an upper bill to use as a probe. In New Zealand, sexual dimorphism in beak morphology of the now extinct Huia (*Heterolocha acutirostris*) allowed pairs to extract food from different parts of a branch and perhaps to feed cooperatively (Buller 1871; Jamieson and Spencer 1996).

Plants exhibit a variety of adaptations to islands. They may lose chemical and morphological defenses against herbivorous mammals (Rhoades 1979; Bowen and Van Vuren 1997). Because birds lack the cutting ability of mammalian teeth, plants may use other strategies such as divaricating growth forms, spines, mimicry, defensive coloration, heteroblasty: changing morphology between juvenile and adult plants, and "playing dead" to reduce herbivory by large herbivorous birds such as flightless moas in New Zealand, elephant birds in Madagascar, and flightless geese in Hawaii (Greenwood and Atkinson 1977; Givnish et al. 1994; Bond and Silander 2007; Fadzly et al. 2009; Berentson 2012). Island plants may acquire secondary woodiness and attendant longevity, allowing them to grow above herbaceous competitors (Darwin 1860; Carlquist 1970; Böhle et al. 1996) and to be pollinated where insects are rare (Wallace 1878).

Plant species may co-evolve with pollinators or seed dispersers, changing seed and flower shape, size, and color, making them dependent on the new pollinators. For example, in New Zealand, the parasitic wood rose (*Dactylanthus taylorii*) is pollinated by the ground-foraging lesser short-tailed bat (*Mystacina tuberculata*) (Ecroyd 1996). In Hawaii, a variety of plants appear to have co-evolved with endemic honeycreeper pollinators (Drepanidini) (Carlquist 1965). Unfortunately, many of the birds are now extinct and the plant species are endangered so we can only infer relationships based on beak and flower morphology (Cory et al. 2015).

5.3.1.3 Behavioral

Behavior may change, such as increasing tameness (Darwin 1839; Cooper et al. 2014), reduced flocking in birds, presumably a reduction in antipredator defenses (Beauchamp 2004), "unwillingness to disperse" or to cross water or other habitat gaps (Darwin 1839; Diamond 1974, 1984; Komdeur et al. 2004) and loss of migratory behavior (Ferrer et al. 2011) as in the Hawaiian Nene (*Branta sandvicensis*) which in turn can lead to flightlessness and speciation (Ripley and Lansdowne 1977).

5.3.1.4 Ecological and Evolutionary

Island birds may be selected for life history strategies with longer life spans, reduced reproductive effort, and later age of sexual maturity, perhaps as a response to limited resources and space (Diamond 1974; Ferrer et al. 2011). To reduce competition or to better exploit resources, species may diverge in how they use such habitats at the macro or micro levels. Divergence might take place in isolation, allopatry, on larger islands or on different islands of an archipelago (e.g., Parent et al. 2016, Fig. 5.3). Species may further diversify within islands as barriers arise following landscape erosion, landslides, or desiccation and consequent separation of once contiguous habitats (Whittaker et al. 2008). This may have occurred among Hawaiian land snails where separate species occupy adjacent ridges (Holland and Hadfield 2002).

All these factors may combine to produce rapid evolution of diverse, endemic species, and "adaptive radiation," found in Galapagos finches, mockingbirds and tortoises, Hawaiian land snails, silverswords and honeycreepers, and Gulf of Guinea white eyes (Zosteropidae) (Darwin 1860; Schluter 2000; Barrier et al. 2001; Carlquist et al. 2003; Melo et al. 2011). While charismatic tortoises, finches, and honeycreepers have been the popular exemplars of adaptive radiation, smaller organisms such as land snails and *Hyposmocoma* moths in Hawaii are much more diverse and are deepening our understanding of species evolution on islands (e.g., Cowie and Holland 2008, Rubinoff 2008; Fig. 5.5).

Speciation and habitat specialization may lead to smaller populations and greater vulnerability to environmental change, arrival of competitors or disease, or increased population variability. This may increase the possibility of extinction over time unless a species can once again expand its habitat and range and become an effective colonist, a concept known as the taxon cycle (Wilson 1961; Ricklefs and Bermingham 2002).

Fig. 5.5 An emerging exemplar of adaptive radiation in invertebrates on islands. Fancy-cased moths *Hyposmocoma* moths in Hawaii have evolved more than 350 species from a single colonizing ancestor. The species manufacture a diverse array of larval protective covers or cases for a range of habitats from freshwater to shoreline to 3000 m (Rubinoff and Haines 2005; Rubinoff 2008) (published with permission of D. Rubinoff https://www.ctahr.hawaii.edu/rubinoffd/rubinoff_lab/projects/Hyposmocoma/hyposmocoma.htm)

5.4 Disease Implications and New Hosts

5.4.1 Consequences of Small Founder Populations

Island colonization tends to be by small groups or individuals, resulting in reduced genetic diversity, more likelihood of inbreeding and genetic drift, and less scope for mutations (Schrieber and Lachmuth 2017). If only a few individuals colonize, they may be less likely to be accompanied by the full suite of parasites that the species hosted on the mainland because not all potential host individuals are parasitized and there may be selection against parasitized individuals being able to successfully disperse (Dobson and McCallum 1997).

Successful colonists may not be exposed to continuing challenges that would strengthen their immune systems against such lost parasites or other challenges, should these subsequently arrive (Spencer and Zuk 2016). The genetic diversity of the parasites that do accompany their hosts may be similarly reduced (e.g., Gage and Kosoy 2005; Minard et al. 2015) but still more genetically diverse than the host species because parasites can escape post-colonization population bottlenecks more rapidly through their shorter lifespans and faster population growth. Finally, single-strand RNA viruses are capable of rapid evolution through genetic drift so they could play roles in species establishment and survival that remain largely unexplored (Chen and Holmes 2006; Holmes and Grenfell 2009; Faillace et al. 2017).

5.4.2 Host and Habitat Switching

At the community level, parasite species may require the same range of suitable conditions as do host species if they are to become established (Blackburn and Ewen 2016). Parasite species that require multiple hosts to complete their life cycles are less likely to be effective colonists. The alternate host has to already be there or the parasite has to adapt to a new one as it arrives (Lymbery et al. 2014).

Parasites may be generalists across their ranges, but specialize on hosts locally (McCoy et al. 2013), potentially priming them to adapt to new hosts after colonization. Ewen et al. (2012) found that *Plasmodium* spp. which successfully established in New Zealand tended to be generalists with a wide range of host species. In contrast, Levin et al. (2016) found that *Plasmodium* in Galapagos did not have a greater host range than on the mainland. Filarial worms, a nematode parasite not uncommon in cormorant relatives worldwide, thus likely arriving to the Galapagos Islands in cormorants, have jumped to the Galapagos Penguin *Spheniscus mendiculus* (Merkel et al. 2007). This jump was probably facilitated by the sedentariness of the Flightless Cormorant *Phalacrocorax harrisi* sharing the same breeding habitat with penguins in the western part of the archipelago (see Chap. 7, this volume).

Parasites may switch habitats and associated hosts. For example, the mosquito *Aedes taeniorhynchus* in Galapagos, having spread inland from its “traditional” brackish water habitat, switched to reptiles from its usual avian and mammalian diet (Bataille et al. 2009; 2012). The Rock Dove protozoan *Trichomonas gallinae* switched to the Galapagos Dove *Zenaida galapogensis* (Harmon et al. 1987). Some apparent parasite switches may actually reflect the arrival of additional parasite strains that can attack new hosts that were resistant to previous strains. In Hawaii, new strains of *Toxoplasma gondii* were associated with mortality of Nene, although the wider demographic consequences need to be investigated (Work et al. 2016).

5.4.3 Migrants

Islands on regular migration routes may be exposed to a regular rain of potential diseases and parasites carried by migrants such that over time the indigenous hosts go extinct, or they evolve to co-exist with the parasites (Laird 1960). Bobolink (*Dolichonyx oryzivorus*) migrating through Galapagos may have served as a pathway for the introduction of *Plasmodium* sp. (Levin et al. 2016). Similarly, migratory birds may have a greater parasite diversity than do more sedentary populations (Jenkins et al. 2012, but see Ricklefs et al. 2016).

Host population structure may also be important on islands, as variable response among multiple small populations may produce rapid selection for resistance that might be slower or impossible in larger, panmictic populations (e.g., Foster et al. 2007).

5.4.4 Ecological Triggers

The arrival of humans with their commensals has frequently unleased new pathogens and parasites into island ecosystems (Goodman 1995; Cheke 2010). This may have occurred so far in the past that we cannot tell immigrant parasite from indigene, even if the initial arrivals triggered drastic “virgin soil” epidemics or even extinctions (Crosby 1976). There are, however, numerous recent or contemporaneous anthropogenic introductions from which to draw insights (Cliff et al. 2000) and the threat remains from future introductions (Dethier 1945; Lounibos 2002; Gottdenker et al. 2005).

Diseases and parasites may invade repeatedly but fail to be established until a vector or alternate host arrives, the invader switches to an alternative host, or until vector populations expand sufficiently to come into contact with potential native hosts. Parasites may also be too virulent in endemic species to become established until more resistant host species arrive that serve as reservoirs, allowing the parasite to persist and spill over in a density-independent manner on the declining native populations (McCallum and Dobson 1995; Woodworth et al. 2005; Sturrock and Tompkins 2008; Lymbery et al. 2014). Alternately, the parasite may evolve reduced virulence over time, although the endemic hosts may not persist during the transition, as may be occurring with the parasitic fly, *Philornis downsi* in Galapagos (Kleindorfer and Dudaniec 2016).

In Hawaii, the arrival of the mosquito *Culex quinquefasciatus* in 1826 provided a potentially effective disease vector that awaited the arrival of poxviruses in the last decade or so of the nineteenth century and introductions of reservoir bird hosts from elsewhere in the early twentieth century to support avian malaria *Plasmodium relictum* (van Riper et al. 1986). These species triggered major mortality and extinctions in native forest birds in Hawaii, eventually restricting many species to elevations above the limits of the mosquito vector (van Riper et al. 1986; Atkinson et al. 2014). The recent arrival (circa 1985) of the same mosquito species in Galapagos may provide an unfortunate opportunity to replicate the Hawaiian experiment, if this mosquito proves a more effective vector than is *Aedes taeniorhynchus* for avian malaria or poxvirus (Whiteman et al. 2005; Parker et al. 2011; Meile et al. 2013). More widely, further arrivals of *C. quinquefasciatus* genotypes on islands may introduce new genes, expanding the distribution of this species from its present peridomestic habitat (Bataille et al. 2009).

Similarly, the arrival of cats (*Felis catus*) across the Pacific allowed the establishment of toxoplasmosis, felids being the definitive host. In island ecosystems such as Hawaii, toxoplasmosis is associated with morbidity and mortality of a range of land and seabirds and marine mammals (Work et al. 2000, 2002, 2016; Honnold et al. 2005; Duffy and Capece 2012). Rats, transported on ships, have brought a wide range of zoonotic pathogens to islands (Gage and Kosoy 2005; Kosoy et al. 2015). They may exchange pathogens with island endemic rodents, leading to emerging diseases for humans (Mumford 1942; Wilkinson et al. 2014), More recently, habitat destruction, whether direct or caused by introduced herbivores, has brought endemic zoonoses into contact with humans and other animals (e.g., Halpin et al. 2007).

5.4.5 Reduced Immunity

Species may change investment in their amounts or types of immunological defenses, depending on the level of parasite challenge (Schmid-Hempel and Ebert 2003). General immune responses may be less costly than the production of specific antibodies (Frank 2000). Beadell et al. (2007) compared the immunology of pairs of endemic and introduced bird species in the Pacific islands with mainland counterparts. Parasite and genetic diversity were reduced in the island species but there was no consistent immunological response. Similarly, Matson (2006) compared pairs of mainland, Hawaii, Bermuda and Galapagos bird species and found no reduction in immunological defenses.

In contrast, within-species comparisons across islands may reveal more consistent patterns. Lindström et al. (2004) found that Galapagos small ground finch (*Geospiza fulginosa*) on larger islands in the archipelago, where parasitism was heavier, had "standing" immune systems that generally mounted nonspecific but faster responses than did the immune systems of finches on smaller islands. Whiteman et al. (2006) found that Galapagos hawks (*Buteo galapagoensis*) had lower genetic diversity, reduced natural antibody response, and higher parasite load on small islands than on large islands. Huber et al. (2010) found that antibody levels in the Medium Ground Finch (*Geospiza fortis*) were higher where poxvirus was observed in birds than where it was apparently absent. Behavior can also play a role. Antibody levels against the parasitic nest fly (*Philornis downsi*) were higher in the finches during the breeding season and higher in females, which do the brooding on the nest (Huber et al. 2010) (Fig. 5.6).

Genetically bottlenecked populations on islands may have lower immune responses to challenges, even if their parasite loads are similar to those in outbred populations (e.g., New Zealand Robin *Petroica australis*; Hale and Briskie 2007), but the consequences may vary between species. For example, absence of particular alleles did not significantly affect vulnerability to malaria in a small population of North Island Saddleback *Philesturnus carunculatus* on Mokoia Island, New Zealand (Sutton et al. 2016).

Overall, the relation between immunity and islands appears complex. Past genetic and parasite history and evolution, tradeoffs in resource allocation, differences between susceptibility and resistance, and difficulties in measurement

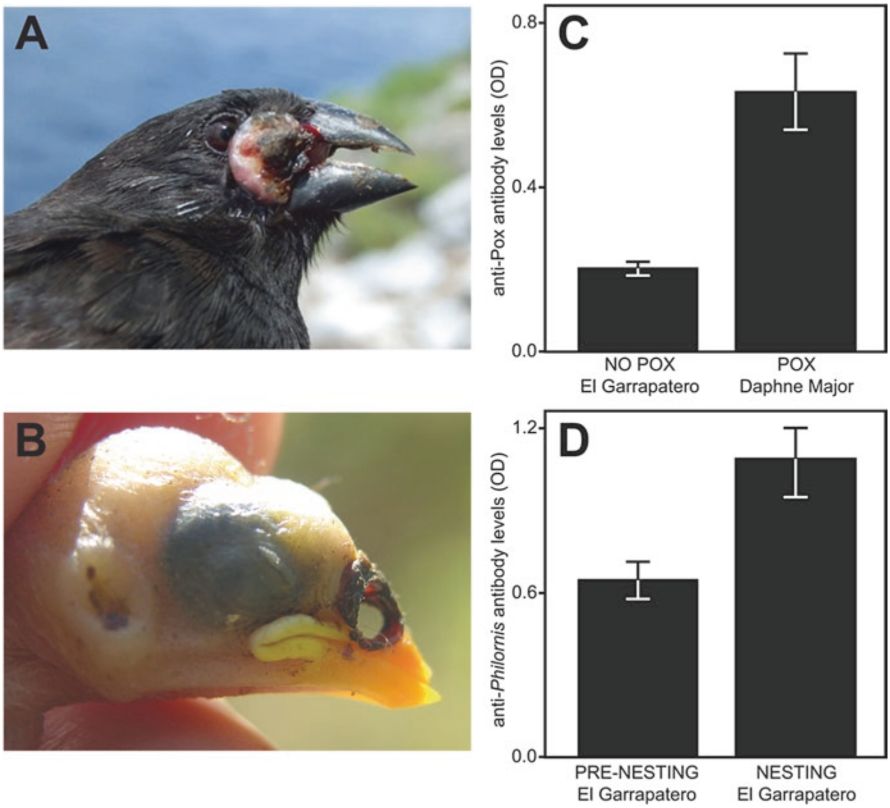

Fig. 5.6 Antibody responses to avian pox and a nest parasite in the Medium Ground Finch (*Geospiza fortis*) in Galapagos (Figure 1 in Huber et al. 2010)

cloud the picture and resist generalization at present (Adamo 2004; Beadell et al. 2007).

Absence or reduced diversity of parasites on islands could allow a newly arrived species to increase its fitness and population growth and reduce the need to invest in costly immune defenses, potentially giving it a competitive advantage against indigenous species (Mack et al. 2000; Blackburn and Ewen 2016). Over time this absence of parasites could make species vulnerable when challenges from old or novel parasites finally arrive and require stronger immunologic responses (Stringer and Linklater 2014), resuming an evolutionary race between a species and its parasites or predators (Van Valen 1973; Dawkins and Krebs 1979). There may also be a tradeoff between the health or fitness of an individual and that of the population which may be especially of concern for the conservation of small island populations (Spencer and Zuk 2016). The end result for island endemics is likely to be a greater vulnerability to the arrival of new competitors or parasites or to environmental change or to some combination of these than for their mainland counterparts (e.g., Blackburn et al. 2004; Fessl et al. 2001).

5.5 Discussion

As in most of ecology, theories on the arrival and establishment of species on islands and the role of genetics and parasites represent a tension between the desire for broad theories and generalizations and the limitations that arise when trying to apply these to particular species, environments and islands (e.g., Simberloff 1976; Case and Cody 1987). While we can make generalizations about island species and their parasites, the reality is that each situation is different, a product of the taxa involved, their colonization, subsequent history, and environment (Hutchinson 1965).

In addition, the study of islands faces the limitations of history (Steadman 1995). Biologists too often arrive after the event so they have to infer behavior or distribution from museum specimens or guess the disease involved, such as those that devastated Native Hawaiians (Schmitt 1970; Bushnell 1993). In the absence of pollen or fossil records, we are often unclear about whether species are indigenous or even endemic, being survivors of a wider distribution in an archipelago. Ideally, as exceptions and complications arise from additional research, they can be incorporated into newer models by intussusception (cf. Deevey 1972).

Enduring areas of controversy concerning island species and becoming sedentary include the extent of speciation in situ, dynamics of species diversity and community assembly, the role of history, the existence and importance of the “island rule” about size changes, and the extent and effects of immunological changes.

5.5.1 Conservation

Most of our theories ignore the role of humans; however, there are now few if any islands that have not been heavily affected by human habitat conversion and destruction and the deliberate or accidental introduction of plant and animal species and diseases (Crosby 2004). Unfortunately, we appear to be in a race to understand island species before they disappear. Island biology runs the risk of becoming solely a discipline of history and paleontology rather than a study of contemporary conditions. As a result, the field has a vested interest in the conservation of islands which may in turn inform conservation efforts.

Biosecurity, identification of species likely to be successful and disruptive invaders, prioritizing habitats and providing the science to manage, restore or protect habitats and species: all require basic science. For example, ex situ conservation needs science to identify which species may benefit from it, the minimum populations needed, and the conditions under which species can be successfully released. Gaining these insights may prove challenging and the results may be counter-intuitive. Captive rearing and reintroductions may lead to inbreeding or to the removal of parasites that stimulate immune systems in rare and vulnerable island species (Stringer and Linklater 2014). Ensuring the health of individuals in captive rearing programs may be counterproductive at the population level in the wild unless there is planned and continuing exposure to parasites (Spencer and Zuk 2016).

Ultimately, with the accidental and deliberate arrival of species, continued human population growth, and anthropogenic climate change, we will live in a panmictic world with less and less room for sedentary/endemic species and habitat diversity. This will be particularly true of oceanic islands. Loss of species may pass largely unnoticed because few people live on or visit islands. Will this loss matter to a growing human population dealing with challenges such as increased drought, rising seas, and the spread of disease? Yes, as islands may be especially useful in studying the ecology and dynamics of epidemics and the emergence of new diseases.

Those who work on islands may be like the monks and scholars who safeguarded Roman and Greek manuscripts at island monasteries following the collapse of the Roman empire (Cahill 1995). They preserved for preservation's sake with no expectation of a future that would later repay their efforts with the flowering of Western science (Lindberg 1992).

Similarly, island biologists and conservationists can only persist while being acutely aware of the ecological losses they can delay but not prevent.

One of the penalties of an ecological education is that one lives alone in a world of wounds. Much of the damage inflicted on land is quite invisible to laymen. An ecologist must either harden his shell and make believe that the consequences of science are none of his business, or he must be the doctor who sees the marks of death in a community that believes itself well and does not want to be told otherwise. Aldo Leopold (1949).

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Part III
Host-Switching

Chapter 6
Host-Switching: How It Starts

Maricruz Jaramillo and José Luis Rivera-Parra

Abstract A parasite depends, during its entire life or at least part of it, on other organisms, but parasites often "jump" from one host species to another and may be able to colonize new host species. The chances of parasite spillover, the first step in such a host switch, may be influenced by factors such as the local ecosystem, community composition, and modes of transmission, among others. In Galapagos, for example, seabirds show a spatially clustered community, with several species that are related and/or nest in close proximity, a seemingly perfect scenario for host switching. However, only one instance of a straggling ischnoceran louse and larva (indicating successful reproduction on the new host) was found on a different host species, suggesting that the specifics of ectoparasite body size and host feather interbarbular space may prevent lice from readily switching hosts. On the other hand, the haemosporidian parasite, *Haemoproteus multipigmentatus*, of the Columbiform-specific sub-genus *Haemoproteus*, was found in significant numbers of Galapagos passerines. The spillover events occur where Galapagos doves (*Zenaida galapagoensis*), a widespread endemic, are present or abundant enough; however, there is no evidence of parasite development in the passerine birds. Thus, the Galapagos archipelago provides an exceptional host-parasite system to investigate details of parasite spillover and its implications for host health and survivorship.

Keywords Avian health • Galapagos • Host switching • Host-parasite interactions • Spillover

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6.1 Spillover

When a parasite finds itself on a host individual that is not of its typical host species, we may call this a host switch. If successful, it could lead to speciation in the parasite lineage, a process that could increase biodiversity in healthy ecosystems (Hudson et al. 2006). When a parasite switches hosts, it changes branches in the tree of life, occupying a different niche and potentially expanding its range. If the isolation from the previous host is relatively strong, it can lead to genetic differentiation and speciation (Ogden and Thorpe 2002; Johnson et al. 2002a, b; Clayton and Johnson 2003; Schluter 2009; Feder et al. 2012). But parasites can jump to other hosts and not establish a viable population. It can be a single individual that jumps and cannot reproduce alone, or the intricacies of host-parasite interaction may hamper establishment of the parasite on the new host; these more temporary relationships are called straggling events (Rozsa 1993; Paterson and Gray 1997; Norton and Carpenter 1998; Ricklefs et al. 2004).

Straggling events may be the starting point of a successful host switch. Parasites that continuously end up in a different host are more likely to end up in enough numbers to establish a population, competing with the native parasites and even evolve to “tweak open” the lock of the host immune system or defense mechanisms (Rozsa 1993; Ricklefs et al. 2004). A major challenge when studying host switching has been to draw a line between a straggling or a host switching event (Rozsa 1993; Whiteman et al. 2004). For the purposes of this chapter, we will define a host switch as having occurred when there is evidence of reproduction (or reproductive stages) in the novel or atypical host.

The chances of parasite spillover, from one host species to another one, are influenced by various ecological and life history traits. Aspects such as niche similarity among host species, modes of transmission, and vector dietary preferences are only a few of the most relevant ones (Rozsa 1993; Johnson et al. 2002a, b; Clayton and Johnson 2003; Whiteman et al. 2004; Bush et al. 2006). We will continue to discuss in detail these and other aspects that may explain the spillover (or straggling) events observed in Galapagos and the ecological and biological factors that explain them. Galapagos is a great laboratory to understand parasite spillover.

6.1.1 Host Community Structure and Transmission

Host-parasite interactions are present throughout the tree of life. The specifics of those interactions depend on the specific host and parasite species involved (Price et al. 2003; Koh et al. 2004; Whiteman and Parker 2005). For example, avian malaria parasites interact directly with the host immune system and need very specific surface proteins to infect the host red blood cells (Valkiūnas 2004). Moreover, these parasites are vector-borne, so they also need a set of proteins that let them infect the arthropod vector, moving through different organs and reproductive phases. In contrast, ectoparasitic avian lice are directly transmitted and barely interact with the host immune system; what they need to be worried about is host preening, which is the main defense mechanism of the host (Price et al. 2003; Whiteman and Parker 2005).

Community composition, its phylogenetic clustering, and similarity of niches among hosts and potential host species define the chances for spillover (Johnson et al. 2003; McCoy et al. 2005; Whiteman and Parker 2005; Hughes et al. 2007; Whiteman et al. 2007). Communities of species that are very distinct phylogenetically or for which related species have very divergent niches, present lower opportunities for parasites to colonize a novel host (Ricklefs et al. 2004). Galapagos shows a very clustered community, with adaptive radiations in the Darwin finches (Lamichhaney et al. 2015), and several species of seabirds that are related and/or nest in close proximity and have significant ecological and social interactions (Baião and Parker 2012; Rivera-Parra et al. 2014).

Having a clustered community is not the only requirement; there must also be real chances for host switching. For example, ectoparasitic lice cannot survive long off the body of the host (Price et al. 2003), so the typical and potential host species must interact physically for the lice to jump from one to the other (Rivera-Parra et al. 2014). Vector-borne parasites such as *Haemoproteus* or *Plasmodium* depend on the dietary preference of the biting insect vector to move across hosts (Valkiūnas 2004; Njabo et al. 2011). Thus, even when there are many potential hosts that have similar niches, there must be opportunities for host switching, through generalist vectors or physical interactions. Depending on the specifics of the transmission mode, there might be even bigger challenges not only for host switching but for parasite survival. For example, if an infected host colonizes a novel environment but there is no competent vector or other competent hosts for the parasite, then the parasite will die off (Telfer and Bown 2012; Inbar et al. 2013; Levin et al. 2013).

Therefore, the way parasites are transmitted across individuals (and potentially across species) is crucial for understanding parasite diversity, specificity, evolutionary history, and chances for spillover (Whiteman and Parker 2005; Rivera-Parra et al. 2015). Roughly, parasites can be classified depending on their transmission as either directly transmitted or vector-borne.

6.1.1.1 Directly Transmitted

Parasitism is a complicated way of life. Parasites depend, during their entire life cycle or part of it, on another organism (Price et al. 2003; Valkiūnas 2004). This makes them vulnerable to stochasticity (e.g., the death of a host before transmission) and even co-extinction (Koh et al. 2004; Whiteman and Parker 2005). Parasites are said to be directly transmitted when they do not rely on other organisms to be vectored from one host to another (Price et al. 2003). Thus, parasites use their own means or their hosts' habits to colonize another individual.

Directly transmitted parasites can take advantage of social interactions to be transmitted (Whiteman et al. 2006). They can be transmitted among independent individuals, which is called horizontal transmission, or they can be transmitted from parents to offspring (vertical transmission; Clayton et al. 1992, Whiteman and Parker 2004). Parasites that are more mobile and/or inhabit social host species or hosts that interact regularly and directly with other potential host species are more likely to spread to novel hosts.

The Galapagos hawk (*Buteo galapagoensis*) is an endemic and diurnal predator of the Galapagos Archipelago (Fig. 6.1). As predators, they interact intimately with their prey, and there is evidence of parasite spillover from their prey to the hawks. Whiteman et al. (2004) found Galapagos dove (*Zenaida galapagoensis*) and introduced goat (*Capra hircus*) ectoparasites on a Galapagos hawk. As the authors suggest, this seems like an example of a parasite straggling. Thus, parasites will survive only for a short period of time and not establish a viable population. The intricacies at play in a host-parasite interaction, such as specific defense mechanisms (like preening) or the host immune system, may prevent a successful colonization, but represent how the host habits create opportunities for parasite spillover.

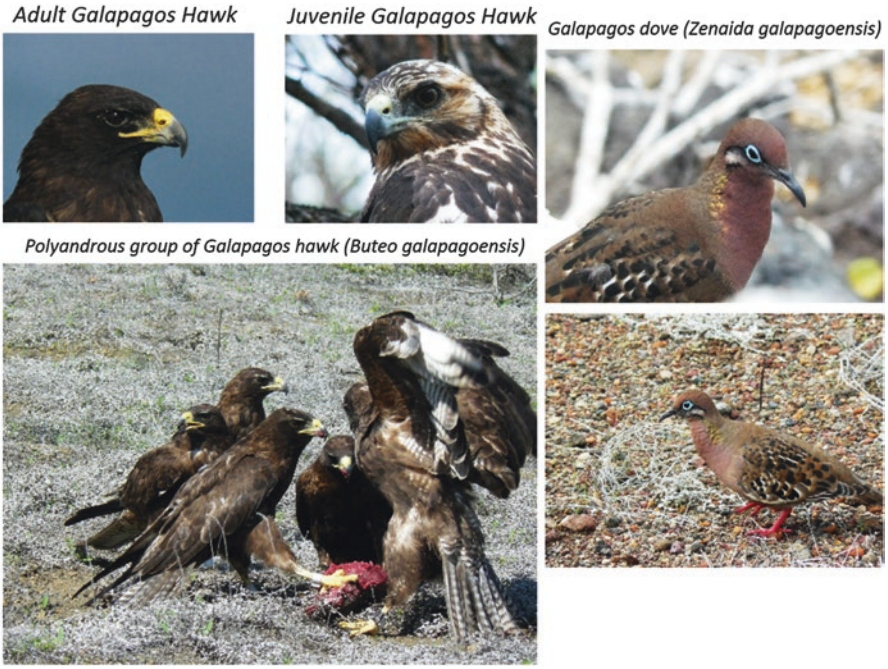

Fig. 6.1 Group of the polyandrous Galapagos hawk (*Buteo galapagoensis*) and their potential prey, the Galapagos dove (*Zenaida galapagoensis*)

6.1.1.2 Indirectly Transmitted

Indirect transmission of parasites usually brings another player into action, the vector. Although this complicates the parasite's life cycle, it also enhances the possibility of transmission as direct contact between hosts is no longer necessary. In the past few decades most emergent infectious diseases that involved wildlife were exotic to the environment in which the epidemic occurred (Daszak et al. 2000; Dobson and Foufopoulos 2001). Even though we would generally expect host-parasite introductions to be greater for parasites with direct life cycles, various co-introduction studies involve parasites with indirect life cycles, the majority of which resulted in host-switches to native hosts (Lymbery et al. 2014). Once parasites are introduced, the potential for pathogen spillover will depend on the host community structure and the presence or co-introduction of alternative hosts or vectors (e.g., Warner 1968; van Riper et al. 1986; Gaither et al. 2013; Novak and Goater 2013).

Spillover occurs when the disease dynamics in one or multiple host populations are driven by transmission from a reservoir host in which the pathogen is highly prevalent, regardless of the mode of transmission (Daszak et al. 2000; Power and Mitchell 2004). Introduced species are often the reservoirs of these pathogens in naive native communities (Lymbery et al. 2014). For this reason, various research efforts in Galapagos have focused on assessing the risk that the poultry industry or backyard chickens pose to endemic wild birds, as introduced chickens may serve as reservoirs for important infectious diseases (Gottdenker et al. 2005; Soos et al. 2008; Deem et al. 2012).

The first evidence of possible spillover of disease from domestic to wild birds in Galapagos was found during a study that assessed pathogens and parasites in chickens and wild birds on Floreana Island, to determine disease risks prior to a possible re-introduction of the endangered Floreana mockingbird (*Mimus trifasciatus*, see Fig. 4.4) (Deem et al. 2012). Thirty percent of chickens presented antibodies against paramyxovirus-1 and 11.3% presented antibodies against adenovirus-2, while for wild birds, prevalence was much lower with only 3% presenting antibodies against paraxymovirus-1 and 2.4% against adenovirus-2, suggesting the direction of transmission from chickens to wild birds. Paramyxovirus-1 and adenovirus-2 are viruses that are transmitted via airborne particles (direct) but transmission can also occur from contaminated surfaces or material or even from fecal matter (indirect). Thus, the potential for indirect transmission of these viruses may increase the risk of transmission from introduced chickens to the endemic wildlife.

Another example of possible spillover from an introduced species to the endemic Galapagos avifauna involves the common protozoan, *Toxoplasma gondii*. Exposure to *T. gondii* has been shown in Galapagos penguins (*Spheniscus mendiculus*) and Flightless cormorants (*Phalacrocorax harrisi*) (Deem et al. 2010). Prior to this study, there had been a single report of a domestic chicken infected with *T. gondii* (Gottdenker et al. 2005). Introduced cats (*Felis catus*) are likely the major reservoir for infection as they are the only host in which sexual reproduction of the parasite is known to occur. Domestic cats on Isabela have been found to have an antibody prevalence of 65% (Levy et al. 2008). Furthermore, it appears that the spillover of disease occurs not only on islands where cats are present, like Isabela, but also on Fernandina, one of the most pristine islands in the archipelago where there are no introduced cats (Deem et al. 2010). Plausible explanations for this observation include but are not limited to: widespread movement of Galapagos penguins (Nims et al. 2008) and dispersal of oocysts by ocean currents (Dubey 2004); attempts to evaluate this mode of dispersal in Galapagos have not been conclusive (Verant et al. 2013). Although *T. gondii* infections are common in many avian species, pigeons and canaries can be severely affected and it can even cause blindness (Dubey 2002). Moreover, *Toxoplasma gondii* poses a significant threat to isolated island avifauna as it has been associated with mortality in several Hawaiian endemics (Work et al. 2000, 2002).

Native species can also become reservoirs for introduced pathogens (Woodworth et al. 2005). In Galapagos, this appears to be the case of the Haemosporidian parasite *Haemoproteus multipigmentatus* and the endemic Galapagos dove (*Zenaida galapagoensis*) (Santiago-Alarcon et al. 2008). *H. multipigmentatus* belongs to the subgenus *Haemoproteus*, thought to be transmitted by hippoboscid flies and previously recorded only in columbiform birds (Valkiūnas 2004; Valkiūnas et al. 2010). Two other species within the subgenus *Haemoproteus* have since been described in Galapagos hosts, *H. iwa* from frigatebirds and vectored by *Olfersia spinifera* (Levin et al. 2011), and *H. jenniae* from swallow-tailed gulls (Levin et al. 2012) (Fig. 6.2); these two species form a deeply divergent sister clade to the hippoboscid-transmitted dove-specific species.

H. multipigmentatus is highly prevalent in Galapagos doves (Santiago-Alarcon et al. 2008) and is transmitted between doves by the endemic hippoboscid fly (*Microlynchia galapagoensis*) (Valkiūnas et al. 2010). *H. multipigmentatus* seems to have a wide distribution in the American continent as it has been found in Mexico, Guatemala, and Peru (Valkiūnas et al. 2010). A phylogenetic study of *H. multipigmentatus* recovered from Galapagos doves and from continental doves suggested that there were multiple events associated with the colonization of the parasite (Santiago-Alarcon et al. 2010, Chap. 7 this volume). The pathogen was likely brought to the Galapagos Islands via domestic rock pigeons (*Columba livia*) which were repeatedly introduced to the archipelago (Harmon et al. 1987; Padilla et al. 2004). Furthermore, sampling of nine pigeons, before they were completely eradicated in 2002, revealed that several individuals were in fact infected with *H. multipigmentatus* (Levin and Parker pers. comm.).

The first report of *Haemoproteus* (*Haemoproteus*) infection in a passerine bird was by Sari et al. (2013), during an effort to elucidate the origin of parasites infecting Galapagos flycatchers, *Myiarchus magnirostris*. Five flycatchers from Santa Cruz Island were infected with *Haemoproteus multipigmentatus* out of a total of 254 Galapagos flycatchers sampled from six different islands in the archipelago. The presence of *H. multipigmentatus* in these birds was detected by molecular methods and examination of the infected blood smears presented no evidence of parasite development (gametocytes were absent), indicating that Galapagos flycatchers may not be competent hosts. Thus, it appeared that the parasites detected in *M. magnirostris* were acquired in the Galapagos Islands by spillover from their reservoir host, the Galapagos dove (Sari et al. 2013).

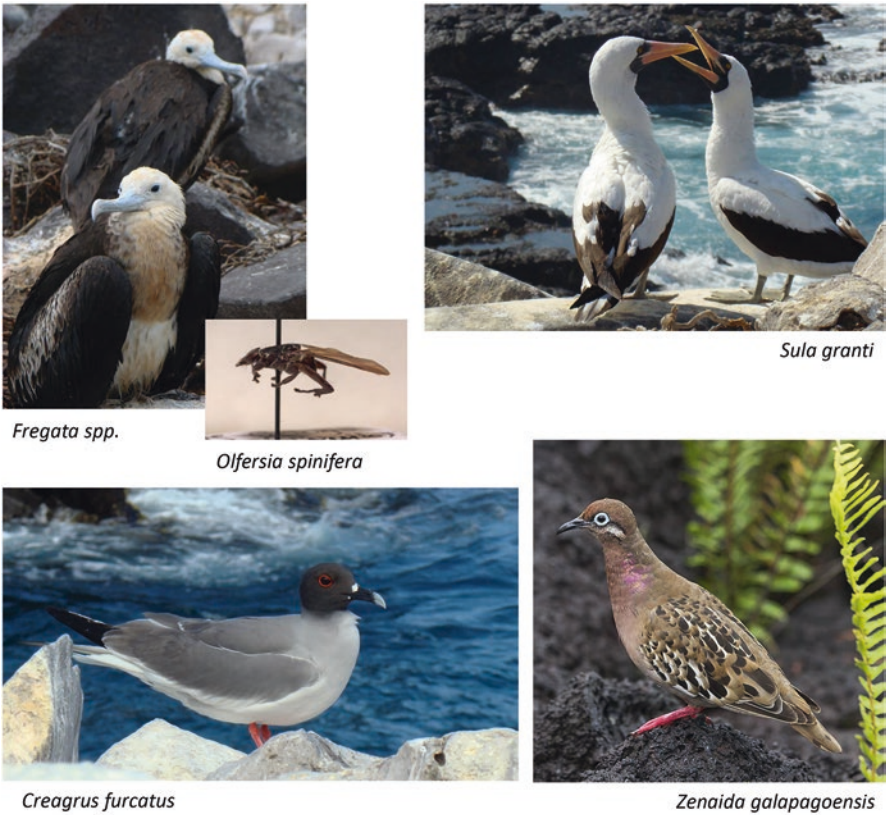

Fig. 6.2 Galapagos hosts reported infected with *Haemoproteus* (*Haemoproteus*) spp. (Photo credits. *Olfersia spinifera*: Manuel Mejía; *Zenaida galapagoensis*: Jeisson Andrés Zamudio; *Fregata* spp., *Sula granti*, *Creagus furcatus*: Maricruz Jaramillo)

An ongoing large-scale avian disease survey that began in 2001 detected *Haemoproteus* PCR signals in passerines but they were not reported because the numbers were usually too small and too scattered to determine the cause of infection (Parker and collaborators, unpublished data). Infected species included a small tree finch (*Camarhynchus parvulus*), a yellow warbler (*Setophaga petechia*), a large cactus finch (*Geospiza conirostris*), seven common cactus finches (*Geospiza scandens*), three small ground finches (*Geospiza fuliginosa*), two large ground finches (Geospiza magnirostris), four Galapagos flycatchers and a vegetarian finch (*Platyspiza crassirostris*) on the islands of Santa Cruz, Isabela, Santiago, Floreana, and Pinta in a span of 6 years.

The most recent avian haemosporidian survey in the archipelago sampled 2254 individuals of 19 endemic and three introduced bird species along an altitudinal gradient in the islands of Isabela, Santa Cruz and Santiago (Jaramillo et al. 2017). The survey revealed 90 PCR positive birds in all years (2013–2015), 89 of which occurred on Santiago. Of these, 31 were Galapagos doves, and the other 58 included small ground finches, medium ground finches (*G. fortis*), large ground finches, a large tree finch (*C. psittacula*), Galapagos mockingbirds, and yellow warblers. These clusters of PCR-positive birds appeared only in locations where doves were also captured and all captured doves were infected (100% prevalence) (Fig. 6.3). Infection intensity in Galapagos doves was generally high, averaging 357 (±307) gametocytes per 10,000 erythrocytes, whereas Galapagos passerines presented no evidence of intraerythrocytic development. This suggests the role of Galapagos doves as reservoir hosts for *Haemoproteus multipigmentatus* in multiple spillover events (Jaramillo et al. 2017).

Although *Haemoproteus* infections have been considered to be relatively benign to their bird hosts (Bennett et al. 1993) or even positive for their lifetime reproductive success (Zylberberg et al. 2015), numerous field and experimental studies have shown the negative effects these parasites can have on birds' fitness (Valkiūnas 2004; Marzal et al. 2005; Møller and Nielsen 2007; Atkinson 2008) and have also been found to be lethal in adapted (Earle et al. 1993) and non-adapted birds (Atkinson et al. 1988; Cardona et al. 2002; Donovan et al. 2008; Olias et al. 2011; Cannell et al. 2013).

Some scientists propose that pathogen spillover from single key host species may be the main source of the parasitic fauna in evolutionarily recent bird communities

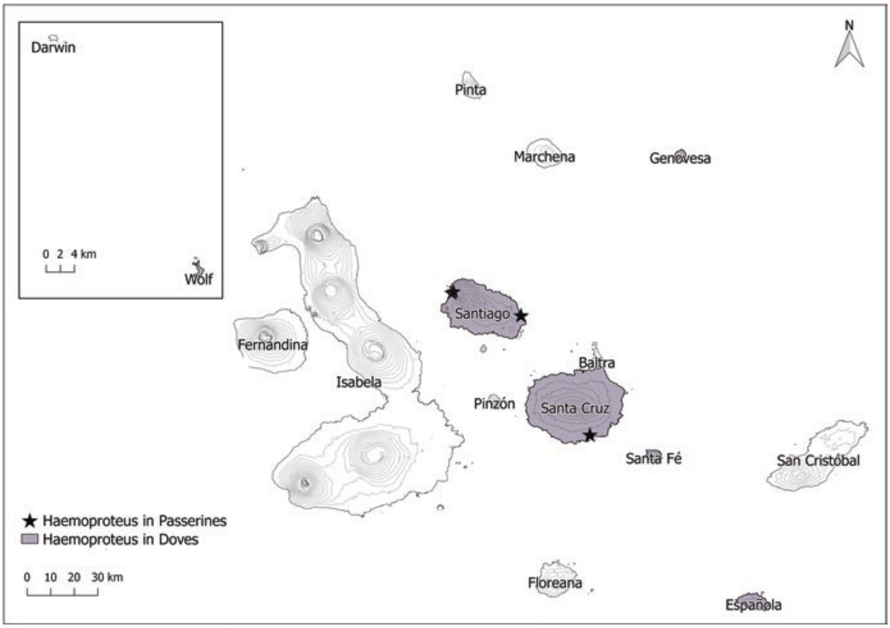

Fig. 6.3 Map of the Galapagos Islands indicating islands (in *grey*) where a study found *Haemoproteus multipigmentatus* in 100% of sampled doves, and sites (*stars*) where it has been found in passerine birds. Galapagos doves are present in all major islands of the archipelago and show high infection at all sampled sites (Adapted from Jaramillo et al. 2017)

(Hellgren et al. 2011). We have reviewed a few examples in which introduced species are likely to be the source for various pathogenic agents found in wild birds in Galapagos (Deem et al. 2010, 2012), and an example of a vector-borne parasite that was likely brought to Galapagos by an introduced dove and whose current reservoir is a widespread Galapagos endemic (Jaramillo et al. 2017). The presence of native alternative hosts and vectors has enabled the spillover of disease to a native community of susceptible hosts. Spillover is the preceding step to host switching, but even if a host switch never occurs, there still might be important effects for the non-adapted hosts and the possibility that these parasites are in turn shaping their hosts' population dynamics.

6.2 Opportunities for Host-Switching

The chances of moving from one host species to another depend on the opportunities the local ecosystem presents. For a successful host-switch to happen there has to be a suitable potential host. This means that the host needs to offer similar "environmental" conditions and similar defense mechanisms (that can be dealt with in a similar way as in the typical host). In addition, there should be enough chances for a parasite to be transmitted across species, so if the parasite is vector-borne, the vector should be more generalist; if the parasite is directly transmitted, the hosts must interact in some way (Whiteman et al. 2004; Whiteman et al. 2005; Rivera-Parra et al. 2015).

Communities that share phylogenetically related species may be more susceptible to host switching, assuming that related hosts maintained similar mechanisms against parasites and share similar niches (Johnson et al. 2003). Niche similarity is relevant because it means more interaction among species. For example, in Galapagos, Darwin's finches are closely related phylogenetically and share the same ectoparasitic lice species (*Brueelia interposita* and *B. chelydensis*; Price et al. 2003). Thus, it seems likely that populations of these two parasites on their hosts have not been sufficiently isolated to allow speciation.

6.2.1 Mixed Species Colonies of Seabirds and Their Lice

Among the rich seabird fauna of the Galapagos archipelago, there are two frigatebirds, magnificent (*Fregata magnificens*) and great (*F. minor*), and three species of boobies, Nazca (*Sula grantii*), blue-footed (*S. nebouxii*), and red-footed (*S. sula*). These five species of seabirds present specific local combinations and degree of spatial overlap. Each seabird species has one specific species of ischnoceran louse, the frigatebirds share an amblyceran louse (*Fregatiella aurifasciata*) and Nazca and blue-footed boobies share another amblyceran (*Eidmaniella albescens*) (Fig. 6.4). In this context, where hosts species nest in close proximity and the lice are

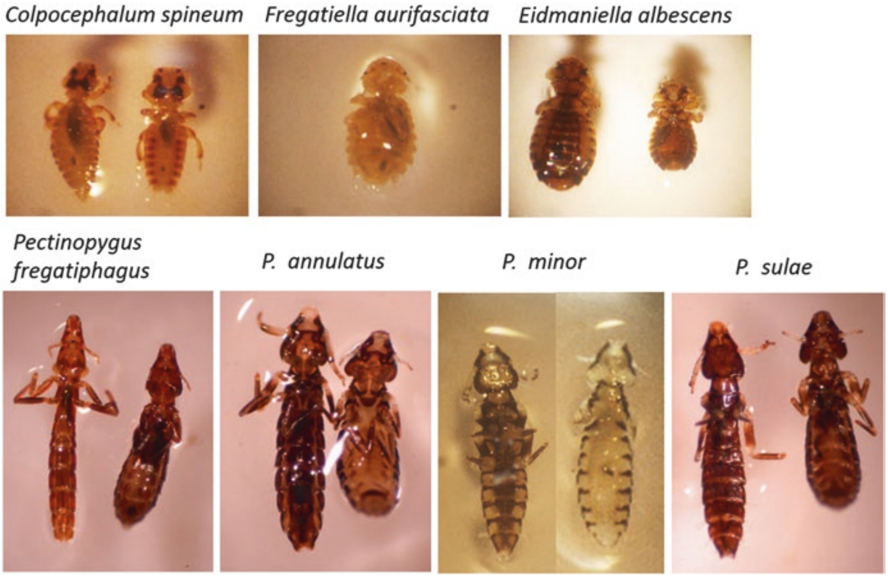

Fig. 6.4 Ischnoceran and Amblyceran lice infecting the three species of boobies and two frigatebirds from the Galapagos Islands. Amblycerans: *Colpocephalum spineum* (commonly infects Magnificent frigatebirds), *Fregatiella aurifasciata* (ex. Magnificent and Great frigatebirds), *Eidmaniella albescens* (ex. Blue-footed and Nazca boobies). Ischnocerans: *Pectinopygus fregatiphagus* (ex. Magnificent frigatebird), *P. annulatus* (ex. Nazca booby), *P. minor* (ex. Blue-footed booby) and *P. sulae* (ex. Red-footed booby)

phylogenetically related or shared, we expected to find a high degree of host switching (Rivera-Parra et al. 2014).

Fregatiella aurifasciata, which was thought to be a single species, showed evidence of genetic differentiation, suggesting lineage sorting, even on the islands where great and magnificent frigatebirds nest together (Rivera-Parra et al. 2015). Similarly, *Eidmaniella albescens* shows two distinct lineages, one in Nazca boobies and the other in blue-footed boobies (Rivera-Parra et al. 2015). Amblyceran lice tend to be highly mobile and transmit horizontally or vertically, but even in this scenario where they could jump from one host to another, they do not seem to do it regularly (Rivera-Parra et al. 2015).

The ischnoceran lice seemed to be extremely specific as well. This system with closely related hosts and parasites seemed perfect for finding host switches, but only a single adult individual and some larvae were found straggling on a different species. Even the effect of neighbor identity did not increase the likelihood of host-switch (Rivera-Parra et al. 2017). It seems plausible that the differences between parasite size (body width) and feather interbarbular space are preventing lice from establishing on a different host. Ischnoceran lice insert themselves in the interbarbular space of the feather as a mechanism of defense against the host's preening; if the parasite is too big, they do not fit and are more easily dislodged (Bush et al. 2006). Boobies plunge dive to fish (del Hoyo et al. 1992), so their ectoparasitic lice have to withstand not only preening by the host, but the forces exerted during the plunge. Thus, any sub-optimal attachment to the feather may result in the lice falling from the host which would prevent the establishment of a viable population.

6.3 Implications for Avian Health

6.3.1 The Immune System of Island Endemics

Biologists frequently believe that isolated island parasite communities are small and impoverished (Wikelski et al. 2004), thus theoretically reducing the number of interactions that occur between parasites and hosts (Hochberg and Møller 2001). The costs associated with maintenance of immune function (Sheldon and Verhulst 1996; Norris and Evans 2000) also suggest that reduced selective pressures, due to low parasite diversity, would result in weakening of the immune system function of hosts through time (Van Riper and Scott 2001; Jarvi et al. 2001). In Hawaii, for example, endemic honeycreepers have been shown to be highly susceptible to introduced pathogens such as *Plasmodium relictum*. The susceptibility of these birds to avian malaria appears to be related to the low genetic diversity of their major histocompatibility complex (MHC) which in turn may reduce antigen recognition and antibody production by the host's immune system (Jarvi et al. 2001).

Loss of MHC and neutral genetic diversity is perhaps an inevitable result of genetic drift for small populations (Sutton et al. 2011) like those found on isolated archipelagos. The Galapagos penguin's (*Spheniscus mendiculus*) population size, for example, was last estimated at 1,500 individuals and it has undergone repeated bottlenecks of about 50% reduction in size every time there is an El Niño event (Vargas et al. 2006). It exhibits low levels of genetic diversity throughout its entire population in the archipelago and presents a lack of population structure among subpopulations (Nims et al. 2008). This low genetic variability can also be expressed at immunological loci that are fundamental in host resistance to disease. Compared to eight other species of penguins, including the Magellanic penguin (*S. magellanicus*) and the king penguin (*Aptenodytes patagonicus*), the Galapagos penguin had the lowest MHC diversity (Bollmer et al. 2007). Hence, the Galapagos penguin has been classified as Endangered (Birdlife International 2016) due to the risks presented by its demographic factors and the genetic monomorphism at loci involved in immune resistance.

Similarly, the endemic Galapagos hawk (*Buteo galapagoensis*) also presented reduced MHC and neutral genetic diversity related to a founder event and subsequent genetic drift, compared to its closest mainland relative the Swainson's hawk (*B. swainsoni*) (Bollmer et al. 2011). Unlike the penguin, the Galapagos hawk exhibits a significant genetic population structure that increases as distance between islands increases (Bollmer et al. 2005; Koop et al. 2014). This structure provided the context for Whiteman et al. (2006) to examine the association between genetic diversity, inbreeding, and disease resistance in the Galapagos hawk. Island populations of hawks with higher degrees of inbreeding presented higher ectoparasite abundance and lower and less variable natural antibody (Nab) levels, demonstrating, for the first time in a wild island endemic, the link between genetic diversity, the innate immune system, and parasitic load.

The relationship between parasite abundance, immunity, and population size has also been investigated for Darwin's finches. Lindström et al. (2004) compared four island populations of small ground finches (*Geospiza fuliginosa*) and found that as parasite prevalence and/or intensity increased with island size, concentrations of natural antibodies and the speed of specific antibody responses also increased with island size. However, the strength of the cell-mediated immune response decreased with increasing island size, presenting an opposite pattern that suggested a tradeoff between antibody and cell-mediated immunity. In environments where parasites are more abundant, it may be more cost-effective to combine the presence of natural antibodies and a rapid production of specific antibodies than to invest in cell-mediated immunity.

A different shift in immune defense strategy of insular versus continental birds was suggested by Matson (2006). His comparison of eight indices of immune function between insular and continental species of birds found that island birds had increased innate and inducible immune responses. Insular birds presented higher concentrations of plasma haptoglobin and elevated levels of two innate leukocytes (heterophils and eosinophils) than continental birds but showed no differences in agglutination and lysis titers (acquired responses). However, Matson warns, the increase in innate responses may be a way to compensate for aspects of insular life such as reduced genetic variation and could possibly intensify the disease risks. In whole, it appears that the relationship between the host's immune system and parasite diversity in island populations is too complex to expect only a simple reduction in immune response in insular birds. Development of the immune system of isolated populations may depend not only on the diversity of parasites present but also on the specific parasites encountered and the stochasticity of mutation and genetic drift (Beadell et al. 2007).

6.3.2 Mortality

Island bird species have shown high vulnerability to introduced parasites. A clear example of this comes from Hawaii, where endemic honeycreepers experimentally infected with *Plasmodium relictum* have been shown to be extremely susceptible to the pathogen, with high mortality rates after a single mosquito bite (Jarvi et al. 2001). Other examples from islands include *Plasmodium* sp. parasites and mortality of native captive birds in New Zealand (Tompkins and Gleeson 2006), and reduced survivorship of endangered pink pigeons (*Columba mayeri*) infected with *Trichomonas gallinae* in Mauritius (Bunbury et al. 2008), among others (Wikelski et al. 2004).

In Galapagos wild birds, documented pathogenic causes of mortality include *Philornis downsi*, avian pox (genus *Avipoxvirus*: Poxviridae), and schistosomiasis (Gottdenker et al. 2008). An experimental approach attributed 27% of nestling mortality to *P. downsi* infestation given that pathogen-reduced nests had three times the nesting success of control parasitized nests (Fessl et al. 2006, see Chap. 9 this volume). *P. downsi* has been found in the nests of 12 introduced, native and endemic species in the archipelago (Fessl and Tebbich 2002) and has been associated with nestling morality in the small (*Geospiza fuliginosa*) and medium ground finches (*Geospiza fortis*) and in the critically endangered medium tree finch (*Camarhynchus pauper*) in Floreana (Fessl et al. 2006; Huber 2008; O'Connor et al. 2010). Avian pox is a prevalent disease affecting a wide variety of Galapagos endemic birds that has been present in Galapagos for at least a century (Parker et al. 2011). High mortality rates had been suggested for young Galapagos mockingbirds (*Mimus parvulus*) given the low recapture rates exhibited by infected individuals (Vargas 1987). Even though *P. downsi* and avian pox are highly prevalent pathogens, these examples constitute the only evidence of disease-related mortality in the avifauna of Galapagos.

Until now, no reports of Haemosporidian infection-related mortality have been documented for any Galapagos bird. Mortality associated with blood parasites in Galapagos wild birds may be underreported or hard to find as most of the Galapagos National Park is uninhabited; moreover, passerine carcasses may be rapidly scavenged by raptors or by feral dogs and cats. However, the potential risks that the parasites reported in the archipelago represent are great as these parasites can be lethal in non-adapted hosts (Atkinson et al. 1988; Jarvi et al. 2001; Cardona et al. 2002; Ferrell et al. 2007; Donovan et al. 2008; Olias et al. 2011; Cannell et al. 2013).

6.4 Concluding Remarks and Future Directions

The Galapagos archipelago provides an exceptional system to investigate the intricacies of parasite spillover. Its simplicity, or low number of host-parasite interactions, compared to continental systems, provides a natural laboratory to determine where the line falls between spillover and host-switching. Future research efforts should focus on determining the effects and risks that each of these events has on host health and survivorship. Furthermore, the link between genetic diversity, the immune system, and disease risk has only been touched and continues to pose very interesting questions about the ecology and evolution of hosts and parasites in isolated ecosystems. The degree of isolation of the archipelago declines with its increasing popularity as a travel destination, which in turn will increase the likelihood for introduced species and pathogens to arrive to the islands and bring ever-increasing opportunities for spillover. Thus, it is of great importance to continue to monitor avian health and pay close attention to ectoparasites and potential vectors of disease.

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Chapter 7
New Host-Parasite Relationships by Host-Switching

Diego Santiago-Alarcon and Jane Merkel

Abstract Host-switching is a natural phenomenon that many parasite species undergo as part of their life cycle; some are highly specialized, but others can readily change hosts to what is available in the community. Rapid environmental changes can open opportunities for host-switches that sometimes turn into important human and wildlife diseases. Island ecosystems contain large numbers of immunologically naive endemic species. The Galápagos Islands still have all their avian endemics extant; however, the ongoing introduction of animals to the archipelago could prompt extinctions of some endemics. In our first example, we tell the story of avian haemosporidian research in the Galápagos, which started with a small number of species, including conservation efforts to safeguard the little known endemic Galápagos dove (*Zenaida galapagoensis*); the work has since expanded to include almost all Galapagos endemics. Our second example will focus on Galápagos penguins (*Spheniscus mendiculus*) and Flightless cormorants (*Phalacrocorax harrisi*) infected by microfilariae (larvae of nematode worms). These two seabird species live in small populations mainly on the rocky coasts of Fernandina and Isabela Islands; they can experience devastating losses during El Niño periods due to food shortages. Fortunately, our studies show that despite high prevalence rates of these parasites, little or no health effect has been detected to date in these three avian endemics. Further monitoring and pathogen research is necessary, however, to rule out conservation concerns related to health effects due to the arrival of additional pathogens, or outbreaks of existing pathogens brought on by environmental change.

Keywords Galapagos endemic birds • Haemosporida • Nematoda • Host-switching • Hemoparasites • Diptera

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7.1 Introduction

Parasitism is the most successful lifestyle on earth; it is estimated that 50% or more of the organisms on the planet are parasites (Poulin 2007). Effects of parasites on host populations and communities can be profound and unpredictable under dynamic circumstances (Hatcher and Dunn 2011). Rapid environmental changes brought about by current human activities are disrupting natural ecological dynamics of both wildlife and their parasites, with unforeseen consequences (Bradley and Altizer 2007; Plowright et al. 2012; Santiago-Alarcon et al. 2015). In particular, land use changes such as agricultural practices and urbanization are among the most worrisome threats to biodiversity conservation and both human and veterinary health (Alberti 2008; Shochat et al. 2010; Aguirre et al. 2012; Hernández-Lara et al. 2017). Most human diseases are zoonotic in origin (i.e., they are derived from domestic and/or wild animals), and many zoonotic diseases are currently emergent threats both locally and globally (Jones et al. 2008). Human encroachment on natural habitats and global trade is rapidly exposing populations of both humans and wild animals to novel parasites that can subsequently develop into pathogens (van Riper et al. 1986; Parker et al. 2006; Alexander et al. 2012; Smith et al. 2012; Suzán et al. 2012; Santiago-Alarcon et al. 2012a). Hence, it is necessary to understand parasite ecological dynamics under the varied array of current environmental changes, in order to be able to predict and prevent parasite host switches that can pose medical and veterinary threats. However, it must be clear that parasites do not only represent negative impacts for their hosts, but they are rather essential components of a healthy functional ecosystem (Hudson et al. 2006; Lafferty et al. 2006, 2008), and deserve to be studied and conserved for their own value (Whiteman and Parker 2005).

In general, host-switching is a natural phenomenon that many parasite species undergo as part of their normal life cycle (e.g., heteroxenous parasites that must pass through two often very different hosts), which has been fine-tuned through time by evolution (Poulin 2007). Many parasites are highly specialized and depend completely on the host species they infect (e.g., lice, Bush and Clayton 2006), but others are more flexible in their preferences and can readily change hosts to what is available in the community (e.g., avian malaria, Ricklefs et al. 2004, Santiago-Alarcon et al. 2014). Rapid environmental changes can open opportunities for host-switches that would otherwise not happen and that sometimes turn into important human and wildlife diseases (e.g., habitat fragmentation, Suzán et al. 2012; wildlife trade, Smith et al. 2012; urbanization, Kilpatrick et al. 2006). For the Galápagos Islands, the most important conservation challenges are posed by an increasing human population and transport (aerial and maritime); the latter is one of the most important reasons for the introduction of pathogens (e.g., avian malaria) into the Hawaiian Islands, which created severe conservation and health problems for the endemic birds (e.g., Drepanididae, van Riper et al. 1986, Atkinson et al. 2000). Nonetheless, host-switches do not necessarily imply disaster for host health and host populations, but rather they are also the way for the development of new associations through adaptive evolution (e.g., aggressive symbiosis hypothesis, Ryan 2009). For example, the endemic Hawaiian bird amakihi (*Hemignathus virens*) has recolonized the lowland areas of the Island of Hawaii, even though avian malaria (*Plasmodium relictum*) is highly prevalent and there is year-round transmission; amakihi individuals still get infected but they experience low-intensity chronic infections, suggesting that this host-parasite interaction has developed into a more benign association (Woodworth et al. 2005). Thus, the lesson is that host-switching events must be studied in a case-by-case scenario, because many host-parasite associations may not respond in an anticipated manner.

Island ecosystems contain large numbers of endemic species, often with small isolated populations, which are often immunologically naive to pathogens, putting them at greater risk than their mainland counterparts (Frankham 1996, 1997, 1998; Szabo et al. 2012). Parasites make their way around the world by natural means, such as with migratory animals, and Galapagos is no exception to this mode of arrival (e.g., Levin et al. 2013, 2016). But avian species in the Galapagos Islands face additional anthropogenic threats due to oil spills, tourism, human population growth, and global climate change (Matamoros et al. 2006). Furthermore, introduction of hemoparasites is a factor that can lead to island extinctions, such as those that have occurred in Hawaiian endemic birds (Warner 1968; van Riper et al. 1986) and endemic mammals on Christmas Island (Wyatt et al. 2008). The Galapagos Islands still have all their endemic avian species extant; however, increasing travel to the islands places endemic species at risk of introduced pathogens (Wikelski et al. 2004; Parker et al. 2006), which are more likely to arrive via non-native avian species such as chickens (Soos et al. 2008) and insect vectors (e.g., *Culex quinquefasciatus*, a competent vector of avian malaria, Whiteman et al. 2005). The ongoing introduction of plants and animals to the Galápagos archipelago must be carefully investigated; fortunately, efforts are being made to combat such problems (Cruz et al. 2005; Campbell et al. 2004; Parker et al. 2006).

Our collaborative multiyear project (16+ years) between the Galapagos National Park (GNP), University of Missouri-St. Louis (UMSL), Charles Darwin Foundation (CDF), and the Saint Louis Zoo (SLZ) works to identify and mitigate the impact of pathogens on Galápagos avian endemics. Prior to our work on the Galapagos Islands, only two other studies had examined parasite presence in Galapagos columbiform birds, where *Trichomonas gallinae* was found infecting non-native rock pigeons (*Columba livia*, Harmon et al. 1987) and a new coccidian parasite (*Eimeria palumbi*) was described from an infected adult of the endemic Galapagos dove (McQuistion 1991). Since the year 2001, we have found haemosporidian parasites in several endemic Galapagos birds (Santiago-Alarcon et al. 2010; Levin et al. 2009, 2011, 2013), trypanosomes in a Galapagos hawk (pers. obs. Merkel), and microfilariae in flightless cormorants and Galapagos penguins, which were originally reported by Harmon et al. (1985) (Merkel et al. 2007), as well as many other viruses, bacteria and ectoparasites in a number of endemic and introduced birds. In addition, we were able to add to the body of literature that refutes the paradigm of a paucity of hemoparasites in seabirds (Greiner et al. 1975; Quillfeldt et al. 2011), which states that blood parasites are rare in seabirds because insect vectors would

Fig. 7.1 Endemic birds featured: (**a**) Galápagos dove (*Zenaida galapagoensis*); (**b**) Flightless cormorant (*Phalacrocorax harrisi*); (**c**) Galápagos penguin (*Spheniscus mendiculus*)

not find suitable habitats in oceanic islands with little fresh water and high winds; however, our efforts to trap mosquitoes have yielded high numbers even in coastal areas that appeared inhospitable to mosquitoes (Merkel, pers. obs.). Thus, we have found *Plasmodium* parasite lineages in penguins (Levin et al. 2009, 2013), and *Haemoproteus* parasite lineages infecting red-footed boobies, Nazca boobies, swallow-tailed gulls, magnificent frigate birds, and great frigate birds (Padilla et al. 2006; Levin et al. 2011).

Avian haemosporidians are vector-borne intracellular parasites that belong to the genera *Plasmodium*, *Fallisia*, *Haemoproteus*, and *Leucocytozoon* (Valkiūnas 2005; Santiago-Alarcon et al. 2012b). This group of parasites can have a range of health effects on their hosts, going from mild (e.g., weight loss, Valkiūnas et al. 2006) to severe symptoms such as hypertrophy of internal organs and hemorrhages that can lead to death (e.g., Palinauskas et al. 2008, 2009, 2011). Some decades ago, it was believed that avian haemosporidians were host-specific (Bennett et al. 1993, 1994), but recent studies have demonstrated that there is little cospeciation between these parasites and their bird hosts; indeed, host-switching is the most common co-phylogenetic pattern recorded and possibly the most important way of diversification for this group of parasites (Ricklefs et al. 2004, 2014; Santiago-Alarcon et al. 2014). Here, in our first example, we will tell the story of avian haemosporidian research in the Galápagos Islands, which started by focusing on the waved albatross (*Phoebastria irrorata*) (Padilla et al. 2003) and with the endemic Galápagos dove (*Zenaida galapagoensis*) (Fig. 7.1a) (Padilla et al. 2004) as a conservation effort to safeguard this little known species.

Our second example will focus on Galapagos penguins and flightless cormorants (Figs. 7.1b, c) living in small breeding colonies on the rocky coasts of the Galapagos, mainly on Fernandina and Isabela Islands. These species can experience devastating losses during periods of El Niño because the rich upsurging waters normally brought by the Humboldt Current come to a halt, making food scarce for sea birds in Galapagos during those periods (Valle 1995; Vargas et al. 2005). Both species of birds were discovered to harbor a microfilarial parasite, potentially from the genus *Paronchocerca*, which has been previously reported to infect a Galapagos penguin in captivity and Anhinga (*Anhinga anhinga*), this last species closely related to cormorants (Chabaud and Ball 1964). *Paronchocerca* spp. often infect species that inhabit the shoreline (Bartlett 2008). It is currently unclear whether this is a case of host-switching or just a parasite with a broad host distribution; however, known *Paronchocerca* spp. are confined within bird families and are not previously reported to switch between families (Bartlett 2008). Filarids have been found in many species of birds with a wide range of pathogenicity, ranging from non-pathogenic to fatal (Simpson et al. 1996). Studies have demonstrated that concurrent infection with more than one hemoparasite may increase the likelihood of pathogenic effects (Davidar and Morton 2006) and cause changes in life history patterns such as decreased parental investment and poor body condition (Merino et al. 2000). In the case of Galapagos penguins this is especially worrisome as this population is also infected with *Plasmodium* parasites. Penguins in captivity are known to be sensitive to avian malaria, often resulting in fatal cases (Graczyk et al. 1994). Hence, it is a conservation priority to determine if parasites are native or recent arrivals to island bird faunas (i.e., host switches) via non-native species.

7.2 Case Studies

7.2.1 The Galapagos Dove (Zenaida galapagoensis) and Haemoproteus parasites

Little is known about the biology of the endemic Galápagos Dove; it is a small dove with sporadic early morphological records (e.g., Ridgway 1897; Gifford 1913; Prestwich 1959), but it has well-established phylogenetic relationships (Johnson and Clayton 2000) and taxonomic determination, with two sub-species currently recognized based on body size (Santiago-Alarcon et al. 2006; Santiago-Alarcon and Parker 2007). Finally, a few aspects of its breeding and feeding biology are known from the population inhabiting Genovesa Island (Grant and Grant 1979). Given this paucity of knowledge and the apparent decline of endemic dove sightings on islands inhabited by humans, the Galapagos National Park and the Charles Darwin Research Station were interested in knowing more on the status of this endemic bird across the archipelago. Hence, we visited eight of the major islands, including Darwin and Wolf, the two most northern islands of the archipelago; we also sampled doves on Santa Cruz and San Cristóbal, which are the two islands with the largest human settlements. We aimed at collecting 30 dove samples per island, and for most islands we reached that number, but for the islands of San Cristóbal and Darwin we were only able to capture two and four individuals, respectively. It became obvious that the endemic dove is common on all sampled islands, except on San Cristóbal where it has always been reported as rare or absent (Santiago-Alarcon et al. 2006; Santiago-Alarcon and Parker 2007). Moreover, our genetic analyses using microsatellites showed that endemic doves have high gene flow across islands (Santiago-Alarcon et al. 2006; Fig. 7.2), but are somehow genetically isolated from the two northern islands of Darwin and Wolf, where doves are also significantly larger in body size,

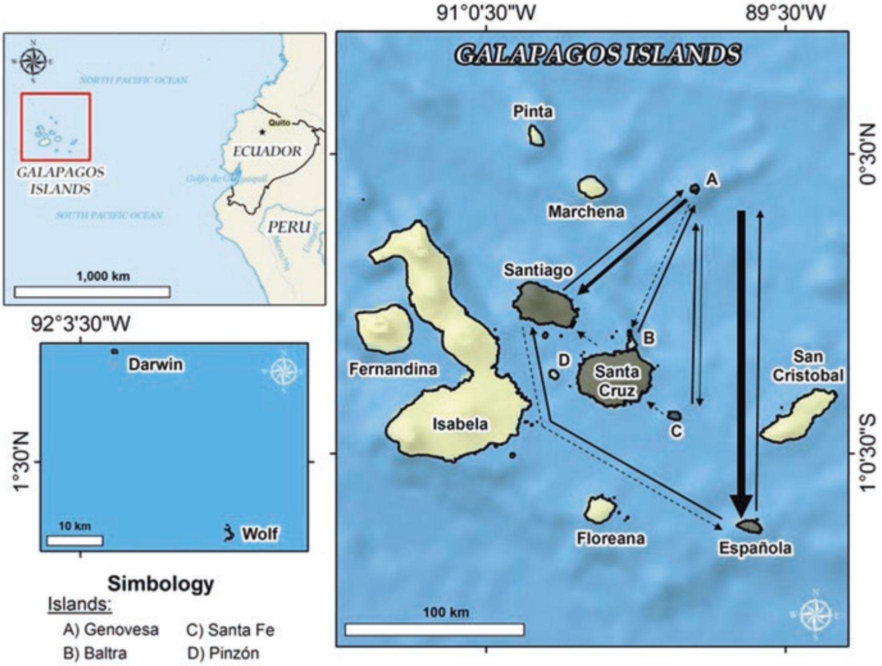

Fig. 7.2 Location of the Galápagos Archipelago and its different islands. Islands in *gray* color are those where Galápagos doves (*Zenaida galapagoensis*) were sampled. *Arrows* indicate microsatellite-estimated gene flow between islands; *arrow* width indicates the amount of directional gene flow

supporting their separation in two subspecies (*Z.g. galapagoensis* and *Z.g. exsul*) (Swarth 1931; Baptista et al. 1997; Santiago-Alarcon and Parker 2007; Fig. 7.3). Subsequently, more microsatellite markers were developed for the *Zenaida* doves (Monceau et al. 2009), which will allow whoever takes the challenge to develop finer population genetic analyses and a deeper understanding of the biology of the endemic dove.

Along with the genetic and morphological analyses of the endemic dove, we took blood samples, cloacal and choanal swabs, and used a pyrethrine insecticide dust to survey for both endo and ectoparasites. In terms of blood parasites, it rapidly became apparent that the endemic dove had an infection prevalence ≥85% for parasites of the genus *Haemoproteus* (Apicomplexa: Haemosporida) on all sampled islands (Padilla et al. 2004). Initial assumptions were that *Haemoproteus* parasites would be more prevalent in the non-native species (rock pigeons) than the resident doves, but no *Haemoproteus* infection was found in any of the sampled rock doves at the time of the study (Padilla et al. 2004). However, we subsequently tested 13 rock pigeons with another set of more sensitive primers, finding six positive infections with the same genetic lineage infecting endemic doves (Parker et al. unpublished). Subsequent molecular work demonstrated that the Galapagos doves

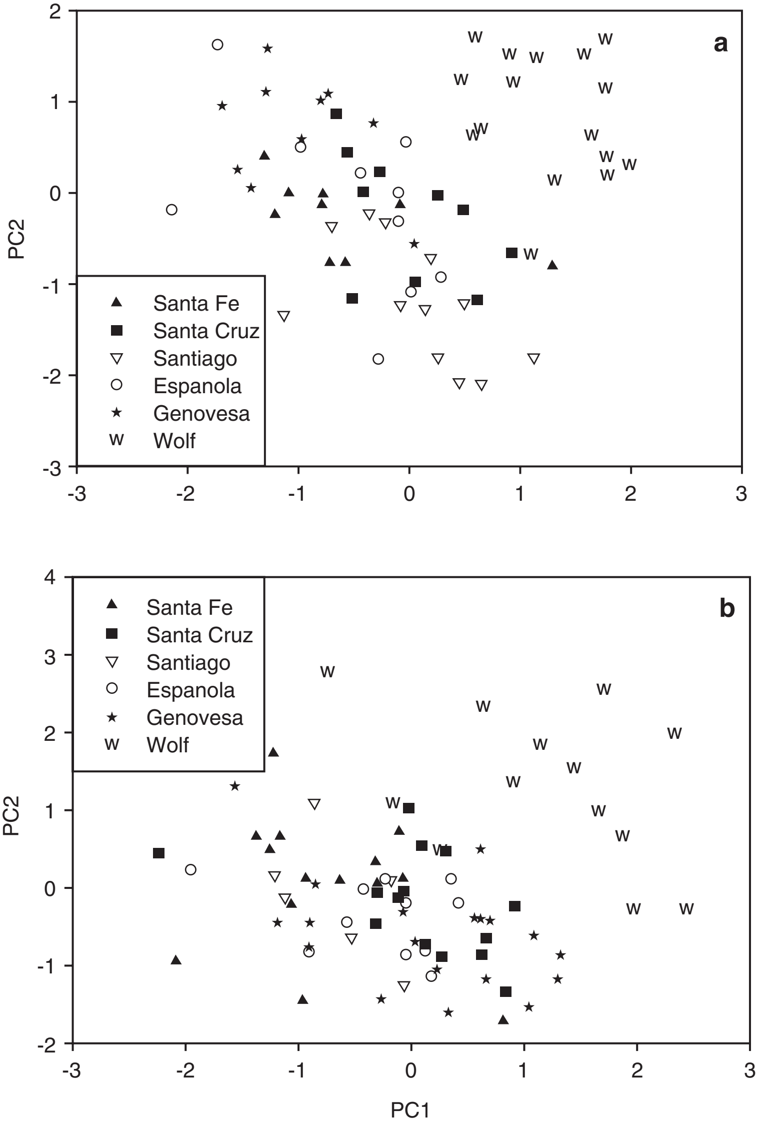

Fig. 7.3 (**a**) Morphological multidimensional space for female Galápagos doves captured on different islands across the archipelago. PC1 axis refers to overall body size and PC2 is an axis representing bill size and tarsus length. (**b**) Morphological multidimensional space for male Galápagos doves captured in different islands across the archipelago. PC1 axis refers to overall body size and PC2 is an axis representing bill size and tarsus length. *Y*-axes from (**a**) and (**b**) have different scales. Birds from Wolf Island (subspecies: *Z. g. galapagoensis*) are significantly larger compared to doves from the southern islands (subspecies: *Z. g. exsul*) (Reproduced from Santiago-Alarcon and Parker 2007)

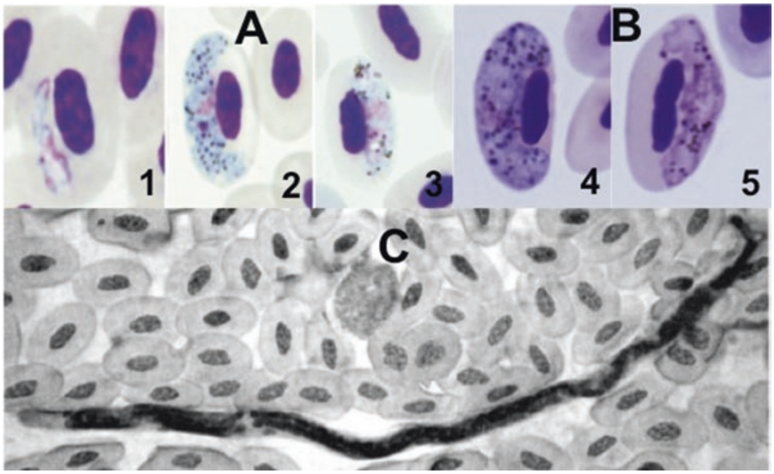

Fig. 7.4 (**a**) *Haemoproteus* (*Haemoproteus*) *multipigmentatus* (a parasite of pigeons and doves): (*1*) young developing gametocyte, (*2*) macrogametocyte, (*3*) microgametocyte. (Reproduced from Valkiunas et al. 2010) (**b**) *Haemoproteus* (*Haemoproteus*) *iwa* (a parasite of sea birds): (*4*) macrogametocyte, (*5*) microgametocyte. (Reproduced from Levin et al. 2011) (**c**) microfilariae (larvae from nematode worms) from a flightless cormorant. (Reproduced from Merkel et al. 2007)

had *Haemoproteus* parasite haplotypes closely related to those found infecting continental doves, suggestive of recent parasite colonization events from either closely related eared doves (*Zenaida auriculata*) or introduced rock pigeons (Santiago-Alarcon et al. 2010). A further investigation of this parasite genus revealed it was a new parasite species, *Hemoproteus multipigmentatus*, which is widely distributed across the American continent (Fig. 7.4a; Valkiūnas et al. 2010; Santiago-Alarcon et al. 2010). Hence, we suggest that *H. multipigmentatus* arrived to the Galápagos with introduced rock pigeons, subsequently switching to the endemic doves, where it is now highly prevalent and produces high parasitaemias, which is a common initial stage of a novel host-parasite association (Altizer et al. 2003; Ryan 2009).

We later sampled sea birds and realized that they were infected by *Haemoproteus* haplotypes that were closely related to the newly described dove parasite, but they were also infected by a unique clade of *Haemoproteus* parasites that was later re-described as *H. iwa* (Fig. 7.4b; Levin et al. 2011). Closely related lineages between endemic doves and different species of sea birds were suggestive of recent host-switches between those two groups of non-passerine birds. Host-switches in this parasite group must be mediated by competent dipteran vectors (Santiago-Alarcon et al. 2012b); in the present case, the putative vectors are three species of louse flies (Hippoboscidae: *Olfersia spinifera* and *Olfersia aenescens* parasitizing sea birds and *Microlynchia galapagoensis* parasitizing endemic doves), a group of blood-sucking flies that do not have specialized host preferences (e.g., Ibáñez-Bernal et al. 2016). Haemosporidian parasites found infecting doves and sea birds belong to the sub-genus *Haemoproteus* (*Haemoproteus*), which is a group that seems to be specialized on non-passerine birds, but that has parasites lineages/haplotypes that appear to readily switch among non-passerine hosts, even hosts that are not closely related (Santiago-Alarcon et al. 2014). For example, *H. iwa* and *H. jenniae* are closely related parasite species that infect birds from different families, Fregatidae and Laridae respectively. Furthermore, the dove parasite *H. multipigmentatus*, which only infects columbiforms, is closely related to lineages (NZB9, CY18, SGT14) that infect birds from different families (i.e., Sulidae, Laridae, Fregatidae) and orders (Suliformes and Charadriiformes) (Santiago-Alarcon et al. 2014). Hence, avian haemosporidians can host-switch across large taxonomic distances, making conservation efforts in the Galápagos and the study of disease ecology more challenging.

Fortunately, indirect evidence suggests that *H. multipigmentatus* do not have a strong negative effect on body condition of endemic doves (Santiago-Alarcon et al. 2012c). Nonetheless, we do not know the real impact of haemosporidians on Galapagos birds, which is a line of research that needs to be developed to gauge conservation efforts of native avifauna. Furthermore, the fact that endemic doves present high rates of gene flow across islands is suggestive of its high dispersal capacity (Santiago-Alarcon et al. 2006), which makes this species both susceptible to introduced pathogens and, if competent, a potential reservoir for moving pathogens across the archipelago that could switch to other endemic birds that are at higher risk due to factors such as small population sizes (e.g., Galapagos penguins; Levin et al. 2009).

Additionally to haemosporidian parasites, we also detected *Trichomonas gallinae* infecting non-native rock pigeons on San Cristóbal Island, but no infections with this parasite were detected in endemic doves from all the sampled islands (Padilla et al. 2004), which contrasts to some degree with the results found by Harmon et al. (1987), where they found infections with *T. gallinae* in three endemic doves from Santa Cruz Island, suggesting a host-switching event from non-native rock pigeons to endemic doves. Rock pigeons have been eradicated from the Galápagos archipelago and are no longer a threat to the endemic dove. We also detected *Chlamidophila psittaci* infecting endemic doves on Española Island, but no introduced rock pigeons, still present at that time, were infected by this parasite; no *Salmonella* sp. infections were detected in either of the two species of columbiform (Padilla et al. 2004).

Finally, we detected high infection prevalence (≥80%) in endemic doves by two lice species native to the Galápagos, *Columbicola macrourae* and *Physconelloides galapagoensis*, which to our knowledge pose no health threat to this bird given that they feed on feathers and feather debris (Santiago-Alarcon et al. 2008). Feather-feeding lice are known to create health problems to their hosts when parasite load is high, producing high levels of plumage damage that can leave birds unable to thermoregulate (Booth et al. 1993). Even in the case of these mostly benign ectoparasites, we have recorded that predator-prey interactions can open the door to host-switching events. We have retrieved the two above-mentioned lice species from endemic Galapagos hawks (*Buteo galapagoensis*), which are known to readily feed on endemic doves, and we know that the only typical bird host of those lice species on the Galápagos is the endemic dove (Whiteman et al. 2004). Hence, different ecological interactions such as competition (e.g., space for nesting on beaches) and predation are likely routes for parasite exchange among birds in the archipelago.

7.2.2 Filarial Parasites of the Flightless Cormorant (Phalacrocorax harrisi) and the Galapagos Penguin (Spheniscus mendiculus)

The Galapagos penguin (*Spheniscus mendiculus*) and the flightless cormorant (*Phalacrocorax harrisi*) have populations of <2000 individuals each (Vargas et al. 2005, Valle 1995; Figs. 7.1b, c). Penguins and cormorants breed and nest on the islands of Isabela and Fernandina; Isabela is an inhabited island with a small human population living near the southernmost tip of the island. Fernandina is considered one of the most pristine islands on Earth due to the absence of human inhabitants or introduced species. Strong El Niño events have a particularly devastating effect on the populations of cormorants and penguins as warmer waters moving from the Equatorial and Panama currents lead to a shortage of fish prey, which are normally brought to the islands via the upsurge of cold water from the Humboldt and the Cromwell currents (Fig. 7.5). Dramatic population declines, as much as 60% of the penguin and 50% of the cormorant populations have been documented (Valle 1995, Vargas et al. 2006). Birds remaining after an El Niño have reduced body condition, which leaves them immunologically suppressed and susceptible to pathogens. Our decision to investigate the disease status of these birds was influenced by the vulnerable nature of their populations. Our goal was twofold: to investigate any current viral, bacterial, or parasitic diseases and to more thoroughly investigate a filarial parasite reported by Harmon et al. (1985).

Trips to collect samples from flightless cormorants and Galapagos penguins were planned over a 2-year period encompassing four collecting trips, two of these in the cool-dry season (August 2003 and 2004) and two in the hot-wet season (March 2004 and February 2005). Throughout the study we collected whole blood, plasma, serum, and swabs from 327 penguins and 448 cormorants. Subsets of samples from penguins and cormorants were tested for viral and bacterial diseases, complete blood counts, and blood chemistry values (Travis et al. 2006a, b). Results demonstrated very little sign of disease in the penguins and cormorants, but we did find microfilariae in both species of birds after microscopic scanning of blood smears (Figs. 7.4c and 7.6). Over the 2-year period, microfilariae prevalence (percentage of infected individuals) increased in cormorants from 33.8% to 59.5% and decreased in penguins from 21.7% to 7.4% (Merkel et al. 2007). In general, cormorants had higher microfilariae prevalence. Parasite intensity (estimated number of parasites per individual) did not differ except in the first season when cormorants

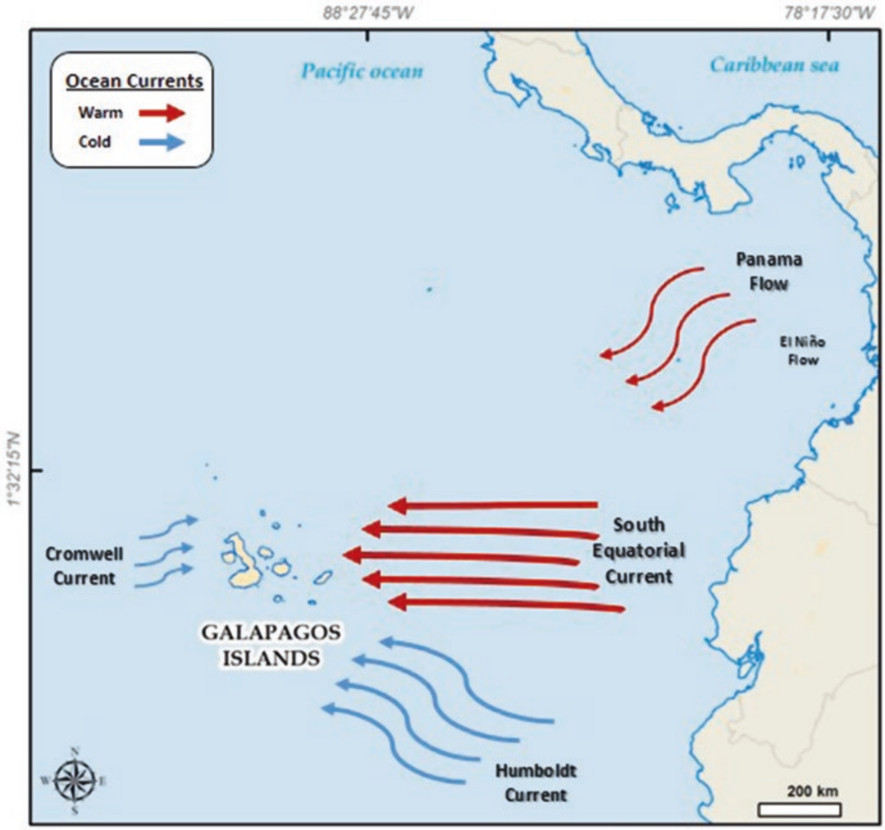

Fig. 7.5 Pacific oceanic currents bringing cold (Cromwell and Humboldt currents) and warm water (South Equatorial and Panama currents) to the Galápagos archipelago

had higher intensities. No relationships between seasonality and prevalence/intensity were found. A few animals of each species that were positive in the first season were recaptured in subsequent seasons and appeared healthy. Morphological methods (Table 7.1) and mitochondrial genotyping determined that the microfilariae from the penguin and the cormorant were the same species of parasite (Merkel et al. 2007). Important issues remain to be studied in this system: (1) the taxonomic description of this novel nematode, (2) pathogenicity on each host species, and (3) if it is not a native parasite, where did it come from? And how did the cormorants and penguins acquire the infection?

Sixteen genera of filarial parasites are known to infect many taxa of avian hosts (Bartlett 2008). Avian filarial parasites can be found in the brain, heart, lungs, spleen, kidney, eyes, subcutaneous tissues, and within the synovial fluid of joints (Bartlett 2008). In many cases no overt signs of disease are present; however, mechanical irritation, dyspnea, anorexia, pneumonia, and lethargy have been

Fig. 7.6 Microfilariae from peripheral blood of the Flightless Cormorant *Phalacrocorax harrisi* (**a**) and from the Galapagos penguin *Spheniscus mendiculus* (**b**). Bar = 50 μm. (Reproduced from Merkel et al. 2007)

Table 7.1 Measurements (μm) of microfilariae from peripheral blood of Flightless cormorants (*Phalacrocorax harrisi*) (*N* = 3 birds) and Galapagos Penguins (*Spheniscus mendiculus*) (*N* = 3 birds) (Reproduced from Merkel et al. 2007)

	Flightless cormorants (*N*: 30)	Galapagos penguins (*N*:21)
Measurements	Mean (range)	Mean (range)
Length	164 (128–184)	164 (136–200)
Maximum width	5.3 (4.0–6.8)	5.3 (4.8–6.0)
Cephalic space	6.4 (4.0–8.8)	5.2 (4.0–8.0)
Nerve ring[a]	25% (18–31%)	24% (20–31%)
Excretory pore[a]	38% (32–47%)	37.6% (32–46%)
Inner body[a]	64% (54–73%)	63% (52–72%)
G 1 cell[a]	74% (63–90%)	75% (62–84%)
Tail	18.1 (12.0–22.4)	19.7 (12.8–29.6)

[a] Proportion of distance from anterior end of microfilariae

reported (Irwin 1975; Bartlett and Anderson 1981; Law et al. 1993; Simpson et al. 1996; Samour and Naldo 2001; Tarello 2006; Larrat et al. 2012). Subtle health compromise in wild birds can be difficult to assess. If the filarial parasite that infects the penguins and cormorants resides in a vital organ, such as the brain or heart, slight health effects could be missed with a single examination. Furthermore, concurrent infection with more than one parasite can have an additive deleterious effect. Mixed infections of an unidentified filarial parasite with *Haemoproteus prognei*, a Haemosporida, have been shown to cause a 90% mortality rate in wild Purple martins (*Progne subis*) (Davidar and Morton 2006). A combination of avian pox and *Plasmodium* parasites, also Haemosporida, had devastating effects on Hawaiian native birds (Warner 1968; van Riper et al. 1986; Atkinson et al. 1995). A *Plasmodium* parasite in the Galapagos penguins, not present in cormorants, was recently detected (Levin et al. 2009; Levin et al. 2013). Serious illness and fatalities have been reported in penguins infected with *Plasmodium* spp. (Fix et al. 1988; Grim et al. 2003; Bueno et al. 2010). Thus, Galapagos penguins concurrently infected with *Plasmodium* spp. and the filarial parasite may be more at risk of morbidity and mortality, but we have no direct evidence of this during the seasons of our sampling.

Filarial parasites have been reported previously in the Galapagos Islands. *Dirofilaria immitis*, a filarial parasite commonly known as canine heartworm, has been found on the island of Floreana (Barnett 1985). Dogs and sea lions were found with circulating microfilariae indicating a patent infection (an infection in which the parasite can complete the lifecycle), while humans and cats demonstrated circulating antibodies (exposure to the parasite but possibly not patent) (Barnett 1985). A subsequent study on Isabela Island, which is inhabited by penguins and cormorants, found that 34% of dogs were infected with canine heartworm. However, it was demonstrated that the filarial parasites infecting penguins and cormorants are unique and only distantly related to *D. immitis* (Levy et al. 2008). Filarial parasites are extremely rare in wild penguins (Jones and Shellam 1999). Our findings of the microfilariae in the Galapagos penguin may be the first in a non-captive penguin species (Merkel et al. 2007). *D. immitis* was found in the heart of a captive Humboldt penguin (*Spheniscus humboldti*), a close relative of the Galápagos penguin (Sano et al. 2005), which was believed to be the cause of death. A different filarioid parasite, *Paronchocera straeleni*, was found in the heart of a Galapagos penguin in captivity; this penguin had been captured in the wild and it was hypothesized that this infection was acquired prior to capture (Chabaud and Ball 1964). Reports of adult filarial parasites in cormorants or closely related birds include *Chandlerella shaldybini*, from a red-faced cormorant (*Phalacrocorax urile*), and an anhinga (*Anhinga anhinga*) infected with *Paronchocerca helicina* (Sonin 1963; Gubanov 1954). The genus *Paronchocera* has 17 identified species known to infect avian hosts (Bartlett 2008). Unlike other genera of filarial parasites which tend to have low host specificity, *Paronchocera* spp. are believed to be host specific within families of birds (Bartlett 2008). Our studies, the life history traits of *Paronchocerca* spp., and the description of *P. straeleni* from a Galapagos penguin has led us to suggest *Paronchocera* as the possible genus infecting both cormorants and penguins. Pending taxonomic validation, this would represent the first report of a *Paronchocerca* species switching between families of birds, Phalacrocracidae (cormorants) and Spheniscidae (penguins). If this is the case and the parasite has switched between families, it is likely that the cormorant is the preferred host. Our reasoning is that (a) cormorants had a higher prevalence of this parasite than the penguins and (b) worldwide, more cormorants are infected with filarids than penguins.

In the case of a parasite with an indirect life cycle it is important to consider possible vectors. All five groups of invertebrates capable of transmitting filarial and haemosporidian parasites to avian species occur in the Galapagos Islands: Phthiraptera (lice), Simuliidae (black flies), Culicidae (mosquitoes), Ceratopogonidae (biting midges), and Hippoboscidae (louse flies). Lice have been documented on both penguins and cormorants: *Austrogoniodes demersus* on Galapagos penguins and *Pectinopygus nannopteri* on flightless cormorants (Palma and Peck 2013; Banks and Palma 2003). Eleven species of ceratopogonid midges occur in the Galapagos Islands (Borkent 1991). Simuliidae are present in the Galapagos; however, due to the lack of fresh water required for breeding, it is unclear whether they inhabit the same coastal habitat as penguins and cormorants (Causton et al. 2006; Peck et al. 1998). There is one native mosquito species on the islands, the brackish-water breeding *Aedes taeniorhynchus*, and two non-native mosquitoes, *Culex quinquefasciatus* (Whiteman et al. 2005) and *Aedes aegypti* (Causton et al. 2006). Larvae of the worm *D. immitis* have been found infecting both *A. taeniorhynchus* and *C. quinquefasciatus* (Barnett 1985). Two different studies have demonstrated that *A. taeniorhynchus* feeds on cormorants (Bataille et al. 2012, Siers et al. 2010) and both have found a DNA sequence of a filarial nematode that was 100% identical to the filarial parasite infecting penguins and cormorants (Siers et al. 2010; Bataille et al. 2012). Siers et al. (2010) found a positive correlation between environmental factors (temperature, vegetation density, moisture) and prevalence. Higher temperatures, precipitation, and ground cover would increase the habitat quality for *Aedes taeniorhynchus*, the putative vector, thereby increasing the likelihood of transmission to the host. Although positive correlations between local environmental conditions and prevalence were found for both species, the correlations were stronger at the cormorant nesting sites (Siers et al. 2010). Lower prevalence in the penguins, despite similar microclimatic conditions for vectors, may point again to the cormorant being the preferred host (Siers et al. 2010). Although *C. quinquefasciatus* can breed in water with up to 40% salinity and is found on Isabela Island, it is improbable that this species is the vector as it is only found in areas close to human habitations or in the highlands far from the penguins and cormorants (Mosha and Subra 1983; Siers et al. 2010).

7.3 Conclusion

Despite more than 16 years of avian parasite research on the Galápagos archipelago, we are barely starting to understand parasite exchange among different host species. There is still taxonomic and systematic work to determine parasite species, their origins, and their health effects on avian endemics. We also need more studies on the ecology and phylogeography of parasites to understand their dynamics, movements, and origins. It is a priority to continue monitoring efforts for parasites across the archipelago, but with particular emphasis on those areas inhabited by humans and visited by tourists. Entry ports, either aerial or maritime, are hotspots for the arrival of non-native species. Hence, if funding for a monitoring program covering major islands is not feasible, then efforts should be made to secure funding for continuously monitoring ports and urban areas. In the case of birds with high dispersal capacity, such as doves, we recommend a continuous monitoring of their populations because they can serve as reservoirs and dispersing agents of non-native pathogens (e.g., avian haemosporidians). In the case of cormorants and penguins, we need to locate recently deceased penguins and cormorants, so we can determine the location of the adult filarial parasite in internal organs, which will allow definitive taxonomic identification. Flightless cormorants and Galapagos penguins are both endangered species (IUCN 2015), and live in restricted parts of a fragile habitat. Hence, we should not assume that these filarial parasites are non-pathogenic, which they may appear to be during benign environmental conditions, especially in the case of immunologically naive island species.

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Part IV
The Spread of Pathogens

Chapter 8
Movement Among Islands by Host, Vector, or Parasite

Iris I. Levin and Arnaud Bataille

Abstract In order to protect the unique fauna of the Galapagos Islands, it is critical that we understand how and when parasites spread throughout the archipelago. There are several key components of host-parasite dynamics that influence parasite spread, including the basic reproductive rate of the parasite, host density, transmission mode, and host movement, among other factors. Host movement could be especially important in determining parasite spread in island systems like the Galapagos, because parasites are not always able to move larger distances unaided. Because some hosts (and vectors) show population genetic structure within the Galapagos Islands, we can make inferences about potential parasite spread from knowledge of host population connectivity. In this chapter, we review patterns of population connectivity in Galapagos vertebrates (hosts), arthropod vectors, and parasites, focusing on population genetic studies. Hosts with little to no population genetic structure and high rates of inferred movement (e.g., Galapagos fur seal, Galapagos penguin, great frigatebird, Galapagos dove, small ground finch, small tree finch, large tree finch) are the most likely to spread parasites. More research is needed on parasite spread, particularly studies that simultaneously estimate population connectivity of both host (or multiple hosts, including vectors) and parasite.

Keywords Connectivity • Population genetic structure • Parasite dispersal • Endemism • Adaptation • Parasite spread

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8.1 Parasite Persistence and Spread

The mechanistic details of parasite spread are of great interest to epidemiologists, theoreticians, and conservation practitioners. Human and wildlife populations are currently experiencing an increase in emerging infectious disease (Daszak et al. 2000; Dobson and Foufopoulos 2001), necessitating a thorough understanding of how disease spreads and what can be done to limit transmission. Throughout this chapter, we will use a broad definition of parasite including viruses, bacteria, protozoans, fungi, as well as more traditionally defined parasites such as arthropods or helminths that depend on a vertebrate host for at least part of their lives.

Parasite establishment, persistence, and spread have been well characterized in mathematical models (e.g., Anderson and May 1986), which can be distilled into several key components. Arguably, the most important variable is R_0, the basic reproductive rate of the parasite, measured as the average number of offspring produced by a single parasite (in the case of macroparasites) or the number of secondary cases of infection caused by a primary infection (microparasites) (Anderson and May 1979). The magnitude of R_0 is proportional to the density of susceptible hosts, and there are critical densities of hosts that result in parasite establishment and spread or extinction (Anderson and May 1986). Critical densities of hosts vary depending on parasite life history and transmission mode. For example, directly transmitted microparasites like viruses typically have large critical host densities because of high host pathogenicity, rapid recovery, and lasting immunity (Anderson and May 1986). Models often include additional variables known to influence parasite dynamics, including the life expectancy of infective individuals, influx of susceptible individuals (via recovery or immigration), transmission mode (e.g., vertical or horizontal), heterogeneous population mixing, and genetic variation in host and parasite populations (Barrett et al. 2008).

Parasite persistence depends on host-parasite dynamics. If transmission is efficient and the infection short-lived, or if there is transmission via long-lived infective stages, the infections tend to be cyclic (Anderson and May 1978, 1979, 1981). Many microparasites exhibit these characteristics, resulting in epidemics and, occasionally, local extinctions in the troughs between epidemics. For example, Bartlett (1960) calculated that cities with greater than 250,000–300,000 people were not likely to have local extinctions of measles, while smaller communities might experience a local extinction for a few years until a new reintroduction of measles. On the other hand, macroparasite persistence is very likely following establishment due to no lasting immunity and typically low host mortality (Anderson and May 1986).

Parasite spread depends on the spatial distribution of hosts, with host movement as a key factor. The spread of rabies in European mammals is a classic example of parasite spread. The epidemic likely originated in Poland in 1939 and was spread primarily by red fox (*Vulpes vulpes*) at an average annual rate of 30–60 km (Anderson and May 1986). This observed rate was corroborated by mathematical models of diffusive transmission, which predicted the velocity of spread by the life expectancy of an infected fox, R_0, and a diffusion coefficient based on the density and movement of foxes (Källén et al. 1985). Another well-characterized example is the arrival of West Nile virus to New York City in 1999 (Anderson et al. 1999). There had been a large outbreak of West Nile virus in Israel that year, and the likely cause of introduction to the United States was an infected traveler (Dobson and Foufopoulos 2001). The mosquito-transmitted virus was spread by at least two species of North American mosquitoes to birds and humans. Within a few years, the virus could be detected in birds throughout most of the eastern United States (Marfin et al. 2001).

8.2 Parasite Spread on Islands

Persistence and spread of parasites in island systems can be different than in mainland systems because there may be larger barriers (ocean or otherwise inhospitable habitat) to host or parasite dispersal between suitable habitat (islands). Spread of parasites between islands involves colonization by host(s) and parasites, either naturally or precipitated by human activity. Parasite life cycle complexity is expected to affect the probability of successful colonization or spread between islands (*see* Chap. 3 for details on parasite colonization). Parasites that must pass through one or more intermediate hosts are less likely to spread unless all necessary hosts co-invade as well (Dobson and May 1986; Torchin and Mitchell 2004). For example, avian malaria (caused by *Plasmodium* parasites), established in Hawaii only after the introduction of the mosquito, *Culex quinquefaciatus* (Warner 1986), and the parasite, which probably arrived with introduced passerine (Long 1981) and migratory birds (Warner 1986). However, it is possible that native hosts can be competent intermediates as well. For example, native copepods have been identified as intermediate hosts for an introduced nematode infecting Hawaiian fishes (Gaither et al. 2013).

Parasite spread in island systems has been documented for several different types of parasites. Tracking spread can be difficult because parasites can go undetected until well after they have spread. However, examining parasite genetic diversity, prevalence, and host-parasite associations can help infer patterns of parasite spread. Insular parasite assemblages are often depauperate compared to mainland assemblages (e.g., Pérez-Rodríguez et al. 2013), host generalists are more likely to establish and spread (Pérez-Rodríguez et al. 2013), and parasites that do establish and spread often show enlarged host breadth on islands (Nieberding et al. 2006; Smith and Carpenter 2006).

The framework provided by MacArthur and Wilson's (1967) island biogeography is well supported by work on parasites and parasite spread in island systems. For example, avian blood parasites in Melanesian islands show a weak species-area association, with larger islands harboring larger numbers of parasite lineages, tracking the stronger species-area relationships in bird and mosquito host species (Ishtiaq et al. 2010). Community similarity (based on the Sørensen index of beta diversity) among bird hosts, mosquito vectors, and *Plasmodium* species parasites decays with distance, evidence for movement by infected hosts—or perhaps more rarely, infected vectors—between geographically closer islands (Ishtiaq et al. 2010). The rate of decay in *Plasmodium* community similarity is twice the decay rate estimated for mosquitoes, which is twice the rate for birds, evidence for either increasing environmental differences with distance, limited dispersal and niche breadth, or both (Ishtiaq et al. 2010).

Some of the best-studied cases of parasite spread involve introduced species and the parasites brought with them. Bluestripe snapper (*Lutjanus kasmira*) was intentionally introduced to Hawaii in 1958–1961, spreading rapidly throughout the archipelago within 34 years (Gaither et al. 2013). This fish likely brought with it an intestinal parasite, *Spirocamallaus istiblenni*, which also infects native Hawaiian fish. Although the bluestripe snapper quickly spread to the tip of the island chain, the parasite has lagged behind, infecting snapper only halfway up the island chain so far (Gaither et al. 2013). Because dispersal of snapper occurs as presumably uninfected pelagic larvae, this pattern is most likely explained by movement of an obligate intermediate host, a native copepod or amphipod (Gaither et al. 2013). When the introduced black rat (*Rattus rattus*) invaded the California Channel Islands, it probably brought a helminth parasite (whipworm, *Trichuris muris*) with it (Smith and Carpenter 2006). This helminth spread to endemic deer mice (*Peromyscus maniculatus*) populations on multiple islands and persisted in deer mice on one island following the eradication of black rats (Smith and Carpenter 2006). Thus, eradicating non-native hosts does not necessarily prevent the persistence and spread of parasites that arrived with the introduced host. However, the deer mice on this island are genetically distinct, suggesting low immigration and emigration to neighboring islands (Pergams et al. 2000), further suggesting that the invasive helminth might not spread to nearby islands that never had black rats to begin with.

Plasmodium relictum spread throughout the Hawaiian Islands, infecting birds in habitats up to an elevation of 1500 m (Huff and Bloom 1935; Huff 1951). Although the vector, *Culex quinquefasciatus*, is found up to elevations of 2500 m (Goff and van Riper 1980), the parasite cannot complete one phase of development in the mosquito (sporogony) below 13 °C, with dramatically slower sporogony at 15 °C (LaPointe 2000). Perhaps not surprisingly, the 15 °C isotherm in Hawaii closely matches the 1500 m contour line, preventing further spread of the parasite and providing refugia for the native species that are particularly susceptible to infection (Atkinson and LaPointe 2009). In summary, research on parasite spread in islands demonstrates that spread requires population connectivity of hosts and all the right "players": definitive hosts, intermediate hosts, vectors, as well as a microclimate suitable for parasite development.

8.3 Predicting Parasite Spread by Studying Host Population Connectivity

In order to predict or mitigate parasite spread, we need to understand host movement. This requires a comprehensive examination of known patterns of population connectivity within the Galapagos Archipelago, focusing in particular on species found on multiple islands. This approach is useful in part because the hosts in Galapagos are, in most cases, far better studied than the parasites. In this chapter, we will review what is known about movement of Galapagos animals throughout the archipelago, focusing on population genetic studies. Population genetic studies infer movement from gene flow, which is an imperfect estimate of movement because movement is only captured when it is followed by genetic exchange. Therefore, estimates of movement from population genetic studies do not account for any animal movements that do not result in interbreeding at the destination. Furthermore, indirectly estimating movement from population genetic data must be done with caution, because the many assumptions associated with the relationship between population differentiation and migration are often violated (Whitlock and McCauley 1999). Despite these caveats, studies of genetic differentiation and population connectivity remain some of our best tools for identifying which animals are likely to move introduced or existing parasites between islands, as mark-recapture programs require intensive efforts and often yield little data in comparison (Whitlock and McCauley 1999). Ideally, both approaches would be employed to give us the most unbiased estimates of host movement.

8.4 Chapter Overview

First, we will provide an overview of population connectivity of Galapagos terrestrial animals, discussing patterns and processes that have caused some groups to radiate since colonization, reflecting very low levels of movement throughout the archipelago; some to differentiate on different islands reflecting some movement; and others that show little to no population genetic structure within the archipelago, reflecting more frequent movement between islands. Next, we will present and discuss what is known about population connectivity and spread of parasite and vector populations in Galapagos, with examples of vector dynamics and movement (*Aedes taeniorhynchus*, hippoboscid flies), vector-borne parasites (microfilariae, avian haemosporidians), non-vector-borne endoparasites (*Toxoplasma gondi*), ectoparasites (Galapagos hawk (*Buteo galapagoensis*) and mockingbird (*Mimus parvulus*) ectoparasites, *Philornis downsi* nest ectoparasites), and bacteria (*Salmonella* in iguanas). Where we can, we will highlight research that examines host and parasite population connectivity; these co-structure studies can often give us the most information about parasite spread. Finally, we will discuss human-facilitated parasite spread in the Galapagos, focusing on the little that is known and the programs in place to combat human-facilitated spread.

8.5 Population Connectivity of Galapagos Terrestrial Animals

The Galapagos archipelago is a rich “natural laboratory” for the study of population differentiation and speciation. Because of the islands’ volcanic origin and geographic isolation, the organisms that currently inhabit Galapagos had to arrive naturally via dispersal or through human introductions. The processes governing the diversification of Galapagos terrestrial fauna have received significant attention and have revealed a number of broad conclusions. First, most of the Galapagos terrestrial fauna that have radiated since colonization have diversified in parallel with the geological formation of the archipelago (Parent et al. 2008). Second, within-island diversification occurs mostly on large islands with diverse habitats in taxa that have very restricted movement (Parent et al. 2008). Third, ecological and habitat specialization play a prominent role in diversification within the Galapagos archipelago (Parent et al. 2008). Another important consideration is the number and timing of introductions (Patton 1984). More recent arrivals have had less time to diversify in situ. There is significant variation in the degree of diversification of Galapagos animals, ranging from species not endemic to the archipelago (e.g., roughly half of insect species) to a radiation of Galapagos land snails with 71 described species (Chambers 1991; Parent and Crespi 2006).

8.5.1 Animals that have Radiated Since Colonization

Relatively few terrestrial lineages have radiated within the Galapagos archipelago; however, because the islands harbor low species diversity, these lineages make up a large proportion of the species on the islands (Parent et al. 2008). Of the two groups of mammals that have colonized (bats, *Lasiurus cinereus* and *L. brachyotis*, and rice rats, *Nesoryzomys* and *Oryzomys* spp.), only rice rats have radiated in situ into at least eight species (Parent et al. 2008). At least 15 subspecies of Galapagos giant tortoises have been described, several of which are extinct, nine subspecies of lava lizards from two separate colonization events now occupy various islands, and there are six species of leaf-toed geckos. There have been two birds that colonized and subsequently formed multiple species: Darwin's finches (14 species) and Galapagos mockingbirds (four species) (Table 8.1). The most spectacular adaptive radiation on the islands is that of the land snails, which have differentiated into at least 71 separate lineages (Parent and Crespi 2006). A number of insects have differentiated since arrival, including microlepidoptera (*Galagete* spp.), weevils (*Galapaganus* spp.), darklings (*Stomion* spp.), and members of *Ammophorus*, *Philantis*, *Scaphytopius*, *Oliarus*, *Pterostichus*, *Dagbertus*, and *Blapstinus* genera (Peck 2001, 2006; reviewed in Parent et al. 2008).

Most of the groups that have radiated since arrival diversified according to the progression of the islands, with the oldest lineages occupying the oldest (eastern) islands, with younger lineages on the youngest islands and sometimes not yet differentiated between some of the youngest islands (Parent et al. 2008). They tend to be more sedentary, so once they arrived on an island they rarely moved to another. Therefore, the result is often one species (or subspecies) per island. In many cases, populations of animals that have radiated throughout the archipelago show evidence of isolation by distance, with more genetic differences built up between islands that are farther apart (Table 8.1). A notable exception to the "progression rule" is the

Table 8.1 Summary of population genetic patterns in Galapagos terrestrial animals, vectors, and parasites

	No. species/ subspecies	No. populations studied	Molecular markers used	No. significant pairwise comparisons	No. genetically unique populations	Evidence for isolation by distance	Range of migration rates	References
Birds								
Galapagos penguin	1 species	5, 3 islands	Microsatellites	0/10	1	No	0.03–0.1	Nims et al. (2008)
Great frigatebird	1 species	5 islands	Microsatellites	2/10	1	No	0.007–0.296	Levin and Parker (2012a)
Blue-footed booby	1 species	3 islands	Microsatellites	0/3	1	Yes, includes non-Galapagos populations	Not given for within Galapagos	Taylor et al. (2011)
Galapagos dove	1 species	5 islands	Microsatellites	0/10	1	No	0.18–1.91	Santiago-Alarcon et al. (2006)
Flightless cormorant	1 species	9, 2 islands	Microsatellites	31/36	2	Yes	Not calculated	Duffie et al. (2009)
Galapagos petrel	1 species	25 colonies, 5 islands	Microsatellites	10/10	3	No	0.003–0.24	Friesen et al. (2006)
Nazca booby	1 species	5 islands	Microsatellites	6/10	3	No	0.003–0.291	Levin and Parker (2012a)

(continued)

Table 8.1 (continued)

	No. species/ subspecies	No. populations studied	Molecular markers used	No. significant pairwise comparisons	No. genetically unique populations	Evidence for isolation by distance	Range of migration rates	References
Yellow warbler	1 species	9 islands	Microsatellites	2/36	3	Not tested	0.012–1.82	Chaves et al. (2012)
Galapagos hawk	1 species	8 islands	Microsatellites, minisatellites	28/28	8	Yes	Not calculated	Bollmer et al. (2005); Koop et al. (2014)
Galapagos mockingbird	4 species	18, 15 islands	Microsatellites	148/153	4	Yes	Not calculated	Hoeck et al. (2010); Nietlisback et al. (2013)
Darwin's finches	14 species	51, 14 islands						Petren et al. (2005); Farrington et al. (2014)
	Geospiza fuliginosa	11 islands	Microsatellites	Not reported	1	Not tested	Not calculated	Farrington et al. (2014)
	Geospiza fortis	12 islands	Microsatellites	Not reported	2 or 4	Not tested	Not calculated	Farrington et al. (2014)
	Geospiza scandens	9 islands	Microsatellites	Not reported	2	Yes	0.0029–0.0074	Farrington et al. (2014); Petren et al. (2005)
	Geospiza magnirostris	10 islands	Microsatellites	Not reported	2	Not tested	Not calculated	Farrington et al. (2014)

	Geospiza conirostris	2 islands	Microsatellites	Not reported	2	Yes	Not calculated	Farrington et al. (2014); Petren et al. (2005)
	Geospiza difficilis septentrionalis	3 islands	Microsatellites	Not reported	2	Yes	0.0007–0.0024	Farrington et al. (2014); Petren et al. (2005)
	Geospiza Difficilis	3 islands	Microsatellites	Not reported	2			Farrington et al. (2014); Petren et al. (2005)
	Camarhynchus parvulus	5 islands	Microsatellites	Not reported	1	Not tested	Not calculated	Farrington et al. (2014)
	Camarhynchus psittacula	5 islands	Microsatellites	Not reported	1	Not tested	Not calculated	Farrington et al. (2014)
	Cactospiza pallida	5 islands	Microsatellites	Not reported	3	Not tested	Not calculated	Farrington et al. (2014)
	Cactospiza heliobates	3 islands	Microsatellites	Not reported	1 or 2	Not tested	Not calculated	Farrington et al. (2014)
	Certhidea fusca	6 islands	Microsatellites	Not reported	5	No	0.00027–0.0034	Farrington et al. (2014); Petren et al. (2005)

(continued)

Table 8.1 (continued)

	No. species/ subspecies	No. populations studied	Molecular markers used	No. significant pairwise comparisons	No. genetically unique populations	Evidence for isolation by distance	Range of migration rates	References
	Certhidea olivacea	6 islands	Microsatellites	Not reported	2	No	0.0010–0.0060	Farrington et al. (2014); Petren et al. (2005)
Reptiles								
Land iguana	2 species	13, 6 islands	Microsatellites	14/15	5	Not tested	Not calculated	Tzika et al. (2008)
Marine iguana	7 subspecies	13	Microsatellites	Not reported	10	Yes	Not calculated	MacLeod et al. (2015)
Lava lizards	9 subspecies	17, 15 islands/islets	Microsatellites	135/136	17	No	Not calculated	Jordan and Snell (2008)
Giant tortoises	11 extant 4 extinct species	11 islands, incl. One extinct pop.	mtDNA	NA	11	Not tested	Not calculated	Poulakakis et al. (2012)
Mammals								
Fur seal	1 species	3, 2 islands	Microsatellites	3/3	1	Not tested	Not calculated	Lopes et al. (2015)
Sea lion	1 species	12, 11 islands	Microsatellites	Not reported	3	Maybe	Not calculated	Wolf et al. (2008)
Vectors, parasites, and pathogens								
Hippoboscid fly *Olfersia aenescens* (host: Booby spp.)	1 species	5 islands	mtDNA	0/5	1	No	Not calculated	Levin and Parker (2013)

Hippoboscid fly *Olfersia spinifera* (host: Frigatebirds)	1 species	5 islands	mtDNA	0/5	1	No	Not calculated	Levin and Parker (2013)
Microfilariae (hosts: Galapagos penguins and cormorants)	NA	2 islands	mtDNA	NA	1	Not tested	Not calculated	Merkel et al. (2007)
Philornis downsi (hosts: Darwin's finches, Galapagos mockingbird and flycatcher	1 species	8, 3 islands	Microsatellites, mtDNA	2/3	2	Not tested	Not calculated	Dudaniec et al. (2008)
Ectoparasitic mite *Myialges caulotoon* (hosts: Cormorants, hawks)	1 species	8 islands (hawks), 2 islands (cormorants)	mtDNA	NA	2	NA	NA	Whiteman et al. (2006a)
Avian pox virus (hosts: Passerine birds, chickens)	NA	2 islands	Viral DNA	NA	3	NA	NA	Thiel et al. (2006)
Salmonella enterica (host: Iguanas)	1 species	5, 4 islands	Genomic fingerprinting (Rep-PCR)	NA	5	Yes	Not calculated	Lankau et al. (2012)

(continued)

Table 8.1 (continued)

	No. species/ subspecies	No. populations studied	Molecular markers used	No. significant pairwise comparisons	No. genetically unique populations	Evidence for isolation by distance	Range of migration rates	References
Nematodes (host: Tortoises)	Multiple	7, 4 islands	Relative no. of egg type	NA	3*	NA	NA	Fournié et al. (2015)
Southern house mosquito, *Culex quinquefasciatus*	1 species	5 islands, airplanes	Microsatellites	9/10	4–5	Not tested	Not calculated	Bataille et al. (2009b)
Black salt marsh mosquito, *Aedes taeniorhynchus*	1 species	32, 8 islands	Microsatellites	119/126	6	Yes, but only tested within 1 island	Not calculated	Bataille et al. (2009a); Bataille et al. (2011)
Ectoparasitic mite (host: Galapagos mockingbird)	1 species	14 islands	mtDNA	NA	7	NA	NA	Štefka et al. (2011)
Feather lice (host: Galapagos hawk)	1 species	8 islands	Microsatellites,mtDNA	28/28	7–8	Yes	Not calculated	Koop et al. (2014); Whiteman et al. (2007)
Body lice (host: Galapagos hawk)	1 species	8 islands	mtDNA	20/28	NA	No	Not calculated	Whiteman et al. (2007)
Hippoboscid fly (host: Galapagos hawk)	1 species	8 islands	mtDNA	16/28	NA	No	Not calculated	Whiteman et al. (2007)

Darwin's finch radiation; other processes appear to have shaped the distribution of finch species and several species are found on multiple islands. Darwin's finches tend to show more pronounced genetic differentiation on either side of the wide equatorial channel separating the main group of islands from the different volcanic province of the northern islands of Pinta, Marchena, Darwin, and Wolf (Farrington et al. 2014). Additionally, there is greater admixture among finches on the smaller, peripheral islands (Farrington et al. 2014). In at least one well-understood case, humans have impacted the population genetic patterns of Galapagos animals. Giant tortoises (*Chelonoidis* spp.) were occasionally moved between islands by humans (Poulakakis et al. 2012), resulting in population genetic patterns that are inconsistent with the diversification hypotheses supported by the majority of the data (Poulakakis et al. 2012).

Animals that have diversified since colonization provide windows into the processes that contribute to speciation, all in a relatively simple environmental context with discrete population boundaries. Because most do not move readily between islands, these groups are not the most likely to spread parasites throughout the archipelago. A notable exception is the Darwin's finches, where most species are found on several islands and there is evidence of some population connectivity (Farrington et al. 2014). However, Galapagos animals that have diversified since colonization often contain multiple small, unique populations found nowhere else in the world, making parasite introduction and spread a conservation concern.

8.5.2 Animals with Evidence for Population Genetic Structure

Population genetic studies of species that occupy multiple islands have revealed varying degrees of genetic structure in the Galapagos archipelago. Several species (Nazca booby (*Sula granti*), yellow warbler (*Setophaga petechia aureola*), Galapagos petrel (*Pterodroma phaeopygia*), and several Darwin's finch species (subfamily *Geospizinae*)) exhibit weak to moderate population genetic structure, forming two or three unique genetic clusters within the islands (Table 8.1). A pattern of isolation by distance is found in half of these species. Species with weak population genetic structure have the potential to move parasites around the archipelago, although some barriers to gene flow (yet not necessarily movement) do exist. Other species are strongly structured, with more than 3–4 genetic clusters (Galapagos hawk, marine iguana (*Amblyrhynchus cristatus*), land iguana (*Conolophus* spp.), sea lion (*Zalophus wollebaeki*)) or show strong genetic differentiation over a restricted range within the archipelago, such as the flightless cormorant (*Phalacrocorax harrisi*). Isolation by distance is found in two-thirds of studies of strongly genetically structured populations (Table 8.1). These species are less likely to spread parasites throughout the archipelago, although immigration/emigration does occur rarely.

Some broad conclusions can be drawn from comparing population genetic patterns among Galapagos organisms that show some population genetic structure.

First, the older, southeastern islands often tend to be the most genetically unique, with low levels of gene flow between southeastern islands and other islands in the archipelago. This could be due to time since colonization; San Cristobal is 3–4 million years old (Geist et al. 2014) with drowned seamounts to the southeast that date back 14 million years (Werner et al. 1999), while Fernandina is between 300,000 and 700,000 years old (Geist 1996). Therefore, populations occupying southeastern islands have had more time to diverge. Although one genetic cluster per island is typically the greatest genetic subdivision identified in nearly all of the species examined, there are two genetically distinct groups of marine iguanas on San Cristobal, likely caused by isolation due to volcanic events (MacLeod et al. 2015). Marine iguanas are strong swimmers, and although they have differentiated throughout the archipelago into multiple subspecies, there is evidence of hybridization between animals from neighboring islands (MacLeod et al. 2015).

Poor dispersal ability can drive genetic differentiation, particularly for islands that are more isolated within the archipelago. Flightless cormorants are unable to disperse even short distances over land and do not typically venture into open water (Harris 1979; Valle 1995). Although they can disperse via swimming 20–30 km (Valle 1995; Vargas et al. 2005), most individuals stay within 2 km of their natal colony (Harris 1979; Tindle 1984; Vargas et al. 2005). This limited dispersal ability explains the strong genetic structure found in flightless cormorants, where all colonies are genetically distinct except from their immediately neighboring colonies (Duffie et al. 2009) (Table 8.1). Galapagos yellow warblers are genetically distinct on two of the more isolated southern islands, San Cristobal and Floreana (Chaves et al. 2012). However, warbler populations on similarly isolated northern islands (Pinta, Marchena, Genovesa) are not distinct from those on the central islands of Santa Cruz, Santiago, Isabela, and Fernandina (Chaves et al. 2012). Smaller, more isolated peripheral islands tend to harbor genetically distinct populations of several of the Darwin's finch species as well (Farrington et al. 2014). Although actual dispersal ability might limit movement between islands and restrict gene flow, dispersal behavior can also shape population genetic patterns. Galapagos hawks, like many broad-winged soaring hawks, are reluctant to cross large bodies of water (Kerlinger 1985). Therefore, they show strong patterns of population genetic differentiation within Galapagos, with unique genetic clusters on every island and low to no gene flow between islands (Bollmer et al. 2005; Koop et al. 2014) (Table 8.1).

Natal philopatry is an important behavioral factor driving population genetic patterns in the two seabird species that show moderate levels of genetic differentiation within the archipelago (Friesen et al. 2006; Levin and Parker 2012a). Nacza boobies are strongly natally philopatric, typically breeding within 100 m from where they hatched (Huyvaert and Anderson 2004) and other species that are closely related to the Galapagos petrel also show strong natal and breeding philopatry (Warham 1990). Neither the Nazca booby nor the Galapagos petrel shows evidence of isolation by distance. Migration rates in the Nazca booby tend to be greater in the southeast to northwest direction, reflecting the prevailing wind patterns and high levels of gene flow—from south to north—found between two of the largest breeding colonies (Española and Genovesa) (Levin and Parker 2012a). Yellow warblers also show the general pattern of south to north gene flow (Chaves et al. 2012).

8.5.3 Animals with Evidence for Little to No Population Genetic Structure

The animals that show evidence for widespread movement throughout the archipelago are ones most likely to be implicated in parasite spread. These include the Galapagos penguin (*Spheniscus mendiculus*), great frigatebird (*Fregata minor*), blue-footed booby (*Sula nebouxii*), Galapagos dove (*Zenaida galapagoensis*), fur seal (*Arctocephalus galapagoensis*), and several Darwin's finches (small ground finch (*Geospiza fuliginosa*), small tree finch (*Camarhynchus parvulus*), and large tree finch (*Camarhynchus psittacula*) (Table 8.1, Fig. 8.1). These animals tend to be very vagile and less natally philopatric.

8.6 Movement of Galapagos Parasites and Vectors

8.6.1 Population Connectivity and Movement of Vectors in Galapagos

In Galapagos, the disease vector most extensively studied in terms of population structure and dynamics is the mosquito *Aedes taeniorhynchus*. This mosquito has strong flying capacity, and, if picked up by wind, can travel over 50 km (Provost 1951; Bello et al. 2005). This is probably how it colonized the Galapagos originally (Bataille et al. 2009a, *see* Chap. 3). The presence of *A. taeniorhynchus* in the air between islands of the archipelago has been documented using aerial nets to sample from boats (Peck 1994), suggesting that the sea does not represent a barrier to their natural dispersal. Population genetic studies later demonstrated that gene flow and inter-island migration occurred frequently for this species (Bataille et al. 2009a, Bataille et al. 2011, Fig. 8.2). Still, *A. taeniorhynchus* populations show significant genetic structure in Galapagos. Mosquito populations from the islands farther apart within the archipelago (Floreana, Española, and Isabela islands) are strongly differentiated genetically (Bataille et al. 2009a). Mosquito populations in the close neighboring islands of Santa Cruz and Baltra are genetically relatively similar to each other, and to San Cristobal Island, but this pattern may be influenced by the boat traffic between these inhabited islands (Bataille et al. 2009a, 2011, see below).

A high level of gene flow was also identified between mosquito populations at either side of the canal separating Isabela and Fernandina Islands. However, an *A.*

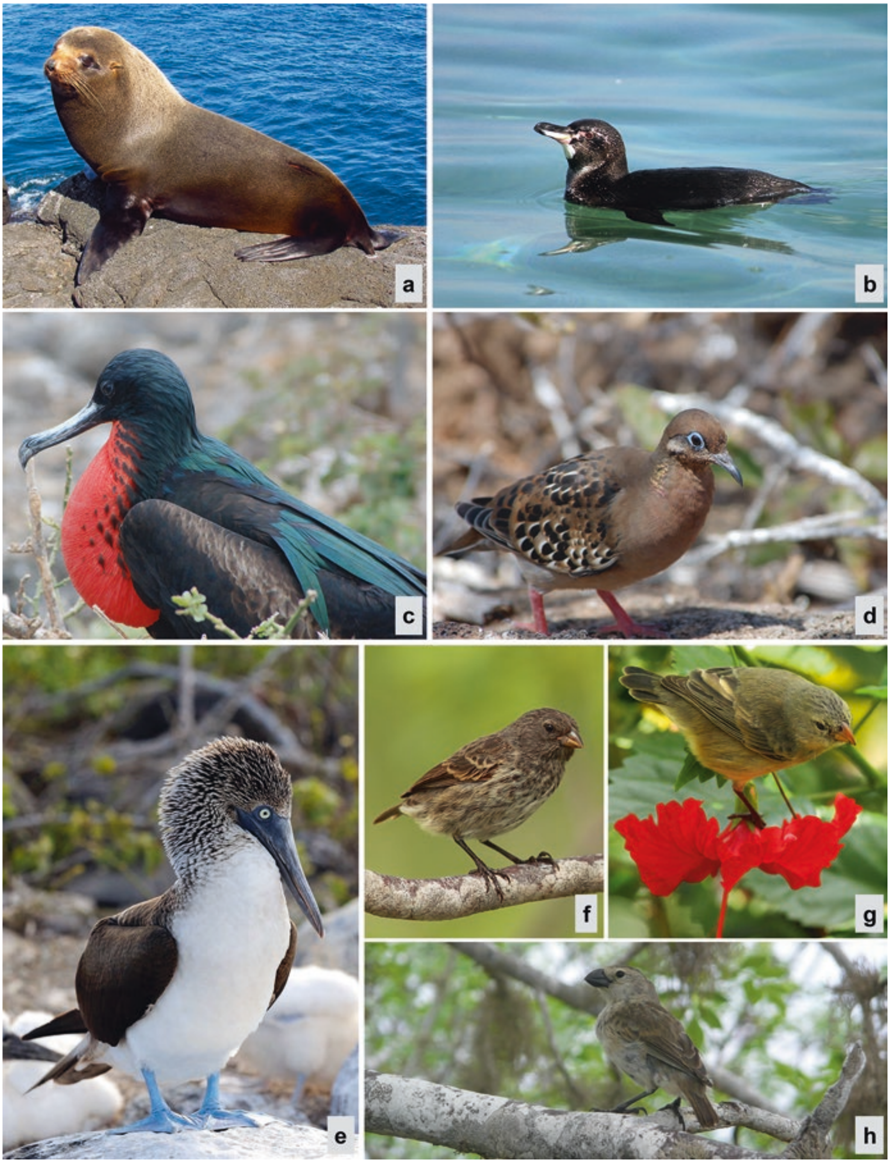

Fig. 8.1 Species with widespread gene flow throughout the Galapagos Islands, suggesting high population connectivity: (**a**) Galapagos fur seal (*Arcocephalus galapagoensis*) photo: D.G.E. Robertson, (**b**) Galapagos penguin (*Spheniscus mendiculus*) photo: C.J. Sharp, (**c**) great frigatebird (*Fregata minor*) photo: I.I. Levin, (**d**) Galapagos dove (*Zenaida galapagoensis*) photo: I.I. Levin, (**e**) blue-footed booby (*Sula nebouxii*) photo: J.M. Pogacnik, (**f**) small ground finch (*Geospiza fuliginosa*) photo: R. Heleno, (**g**) small tree finch (*Camarhynchus parvulus*) photo: R. Heleno, (**h**) large tree finch (*Camarhynchus psittacula*) photo: R. Heleno. Photos have been reprinted with permission of photographer or under a Creative Commons License

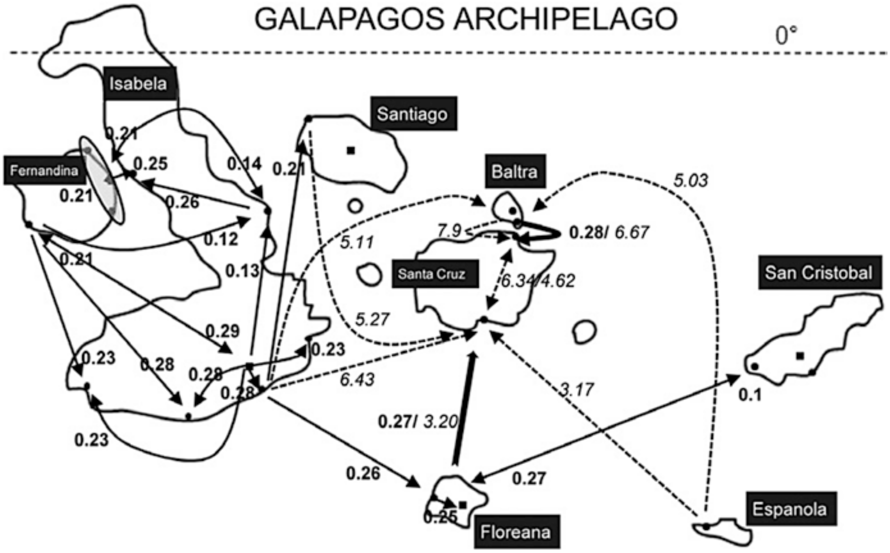

Fig. 8.2 Map of the Galapagos Islands summarizing the direction of gene flow between *Aedes taeniorhynchus* populations as estimated using MIGRATE (effective number of migrants, $4N_em$, numbers in italic, *dashed arrows*) and BAYESASS (migration rate m, *plain bold numbers and arrows*). Thick arrows correspond to movements detected using both BAYESASS and MIGRATE. Some arrows are drawn as *ellipses* to improve the clarity of the figure. Figure is reprinted with permission from Bataille et al. 2011

taeniorhynchus population sampled further away from the canal, on the southwestern tip of Fernandina, diverged strongly from the canal populations, suggesting that local wind patterns may hinder migration in some directions (Bataille et al. 2011). Interestingly, these patterns of *A. taeniorhynchus* gene flow precisely match patterns of microfilarial nematode prevalence in flightless cormorants (*see* Sect. 8.6.2).

Aedes taeniorhynchus population dynamics also vary between coastal and highland habitats of the Galapagos Islands. Highland populations of this mosquito in Santa Cruz, San Cristobal, and Santiago islands are genetically more similar to each other than to coastal populations of their respective islands (Bataille et al. 2009a). These results have led the authors to suggest that this mosquito, typically a specialist of coastal environments, has radiated and adapted to different ecological niches after its colonization of the archipelago (Bataille et al. 2009a). This question was further explored in a subsequent study that focused on the variation in population structure and gene flow through time between coastal and highland mosquitoes of Santa Cruz Island (Bataille et al. 2010). The authors showed that highland and coastal populations were highly differentiated throughout the year, although some gene flow between the two habitats could be detected during periods of higher precipitation. No first or second-generation hybrids between coastal and highland populations could be identified during this study, suggesting that pre-mating isolation barriers may have evolved between these populations.

Mosquito population dynamics on the coast and in the highlands also appear to be differentially affected by environmental conditions. The height of the tide is the main factor influencing mosquito abundance on the coast, whereas mosquito populations were dependent on precipitation patterns in highlands (Bataille et al. 2010). Thus, dynamics of mosquito-borne diseases might be very different between habitats in Galapagos. A parasite could probably be spread more easily along the coast by *A. taeniorhynchus* before it has the opportunity to infect hosts inhabiting highland habitats. Unfortunately, this hypothesis has not been tested in any host-parasite system of the archipelago. Parasite spread between habitats may be less frequent, but is still possible, especially during periods of high precipitation. For example, a mosquito containing blood of marine iguana was collected in a highland site frequented by Galapagos tortoises, 20 km from the coast (Bataille et al. unpublished results), suggesting that parasites of reptiles such as hemogregarine parasites (*see* Chap. 3) may be spread by this mosquito across habitats and across hosts.

The only other Galapagos parasite vectors for which we have population genetic information are two species of obligate ectoparasitic hippoboscid flies, *Olfersia aenescens*, which lives on booby hosts and *Olfersia spinifera*, which parasitizes frigatebirds. These species are long-lived, blood-sucking flies with fully formed wings that spend all but one brief life stage among the host's feathers. We are confident in their role as vectors of *Haemoproteus* spp., blood parasites that are related to *Plasmodium* spp. parasites. DNA from *Haemoproteus iwa*, which is reported to infect frigatebirds around the world, can be amplified reliably from *Olfersia spinifera* thoraxes without simultaneous amplification of frigatebird DNA that would otherwise indicate the presence of the parasite in the blood meal (Levin and Parker 2012b, 2014). Flies can be found on nearly all Galapagos frigatebirds, and the prevalence of *Haemoproteus iwa* is approximately 50% in Galapagos great frigatebirds (Levin and Parker 2012b). Unlike Galapagos mosquito populations, population genetic studies of *O. spinifera* and *O. aenescens* reveal that the fly populations are not genetically distinct on different islands (Levin and Parker 2013). Instead, flies appear to exchange genes with flies from different island populations, even in cases where there is little gene flow between hosts (Levin and Parker 2012b, 2013). Parasites in the subgenus *Haemoproteus haemoproteus* are not typically pathogenic and there is little evidence of a cost of infection in infected seabirds (Padilla et al. 2006). Hippoboscid flies (and the lineages of *Haemoproteus* they vector) are often host specific (e.g., Levin and Parker 2013); therefore, widespread movement throughout the Galapagos archipelago does not necessarily pose a risk of further parasite spread. Furthermore, flies infected with *Haemoproteus iwa* are less likely to switch host individuals than uninfected flies (Levin and Parker 2014). This phenomenon may explain why flies parasitize nearly all frigatebirds and yet only 50% of frigatebirds are infected with the blood parasite (Levin and Parker 2012b, 2014).

8.6.2 Population Connectivity and Movement of Vector-Borne Parasites in Galapagos

Aside from mosquitoes and some ectoparasites, there have been few population genetic studies of parasites and vectors in the Galapagos Islands. However, there are a number of phylogenetic or phylogeographic studies that are informative for making inferences about parasite spread. Many of these studies report genetic lineages of parasites or vectors per host species and island. There are two closely related species of *H. haemoproteus* found infecting seabirds in the Galapagos (Levin et al. 2011, 2012). *Haemoproteus iwa* infects great and magnificent frigatebirds (*Fregata magnificens*), with just one genetic lineage reported from all sampling locations within the archipelago (Levin et al. 2011). *Haemoproteus jenniae* infects the endemic swallow-tailed gull (*Creagus furcatus*) (Levin et al. 2012). *Haemoproteus jenniae* is closely related to *H. iwa* and most likely vectored by a currently unidentified hippoboscid fly (Levin et al. 2012).

The seabird *H. Haemoproteus* species are sister to a clade of dove-specific *H. Haemoproteus multipigmentatus* parasites (Valkiunas et al. 2010; Levin et al. 2011) which are also hippoboscid-transmitted (with *Microlynchia galapagoensis* as the probable vector in Galapagos) and infect a variety of New World dove species including the endemic Galapagos dove (Santiago-Alarcon et al. 2010). *Haemoproteus multipigmentatus* lineages infecting Galapagos doves belong to four clades that also contain lineages recovered from doves sampled in South America, suggesting that there have been multiple colonizations of *H. multipigmentatus* lineages from the continent to the Galapagos (Santiago-Alarcon et al. 2010; *see* Chap. 3 for more information about parasite and vector colonization). Within the archipelago, the lineages show no geographic structure and are only weakly differentiated from continental lineages, suggesting that these blood parasites may have arrived more recently than the dove host (Santiago-Alarcon et al. 2010). The lack of genetic differentiation of dove blood parasites within Galapagos is consistent with the lack of genetic differentiation in the host, suggesting that lineages are spread throughout the archipelago by the mobile host. Similarly, a *Plasmodium* sp. parasite has been repeatedly sequenced from the Galapagos penguin samples and the one genetic lineage has been detected in all but one of the Galapagos penguin populations (Levin et al. 2009). Like Galapagos doves, Galapagos penguins show strong population connectivity, conducive to parasite spread.

Blood parasite spillover has occasionally been documented in the Galapagos. A *Haemoproteus* lineage very closely related to *H. multipigmentatus* was found in one Nazca booby and one swallow-tailed gull sample, but no spillover was documented in the other direction (Levin et al. 2011). Spillover of *H. Haemoproteus* species is rare because of the high host specificity of the hippoboscid fly vectors. Although approximately half the frigatebirds in Galapagos are infected with *Haemoproteus iwa*, no Nazca or blue-footed booby was ever found infected with this species, despite the fact that they often nest in close proximity. It is possible that *M. galapagoensis*, the hippoboscid implicated as a vector of *H. multipigmentatus*, is less host-specific than either *Olfersia* species. Two lineages of *Plasmodium* blood parasites have been amplified from a small number of Galapagos finch or yellow warbler hosts each at one site and in 1 year (Levin et al. 2013). These DNA lineages have also been amplified from North American breeding bobolinks (*Dolichonyx oryzivorus*), which regularly migrate through Galapagos en route to overwintering grounds in South America (Levin et al. 2013). Although it is not confirmed, these instances could also represent parasite spillover. Parasite spillover in Galapagos is covered extensively in Chap. 6.

Galapagos flightless cormorants and penguins have been found infected with a shared species of microfilarid (nematode) (Merkel et al. 2007). Cormorants had higher prevalences than penguins and male penguins were more likely to be infected than females (Merkel et al. 2007). Although unconfirmed, *A. taeniorhynchus* is the likely vector of this microfilarid; the patterns of population genetic structure match the prevalences of microfilarids on Isabela and Fernandina, where Galapagos penguins and cormorants nest (Merkel et al. 2007; Siers et al. 2010; Bataille et al. 2011). Furthermore, DNA matching filarial nematodes was amplified via PCR from a pool of *A. taeniorhynchus* thoraces from mosquitoes collected on Fernandina (A. Bataille unpublished data). The mosquito is widespread and shows evidence of migration between islands within the archipelago (Bataille et al. 2011). However, it is currently unknown whether this microfilarid can infect any other Galapagos host. Flightless cormorants pose a smaller risk of spread than penguins, which appear to move far more frequently between breeding sites throughout the archipelago (Nims et al. 2008).

8.6.3 Population Connectivity and Movement of Non-Vector-Borne Parasites in Galapagos

For directly transmitted parasites, their spread will depend on their own capacity or the capacity of their hosts to travel across islands and across habitats within the archipelago. Some ectoparasites have the capacity to disperse across islands actively or with the help of wind, and this capacity is reflected in their population structure patterns.

Toxoplasma gondii is a common protozoan parasite that can infect a wide range of warm-blooded animals, although the only known definitive hosts are Felids. Sixty-three percent of cats sampled on Isabela during a neutering campaign had antibodies against *T. gondii* (Levy et al. 2008). There are many feral cats on several Galapagos Islands and these animals probably come in contact with wildlife. Galapagos flightless cormorants and penguins tested positive for *T. gondii* antibodies at sampling locations on Isabela, where cats are present and Fernandina, which is cat-free (Deem et al. 2010). *Toxoplasma gondii* antibodies have also been detected in one Galapagos hawk from the island of Santiago, where there is no human settlement and there are supposedly no feral cats (Deem et al. 2012), as well as in one chicken (Gottdenker et al. 2005). *Toxoplasma gondii* oocysts may spread via waterborne transmission; *T. gondii*-like oocysts were detected in water samples from San Cristobal and Santa

Cruz, however PCR tests for the parasite did not confirm the presence of the parasite (Verant et al. 2014). Details regarding *T. gondii* spread throughout the archipelago are lacking. Of the avian species where antibodies have been detected, the Galapagos penguin is the only host that moves frequently among breeding locations. Furthermore, 95% of the penguin population is restricted to Isabela and Fernandina, with only small populations on Floreana and Bartolome (off the coast of Santiago), further restricting the possibility of extensive spread throughout the archipelago.

An introduced parasitic fly, *Philornis downsi*, infects passerine bird nestlings and has been most well studied in Darwin's finches (e.g., Dudaniec et al. 2008; Kleindorfer et al. 2014). The fly was first documented in the islands in 1997 and has been found in finch nests on 11 of the major islands in nests of 14 endemic species (Fessl and Tebbich 2002; Dudaniec et al. 2006). The fly larvae feed on nestlings and cause high mortality (Fessl and Tebbich 2002). A population genetic study of Galapagos *P. downsi* was conducted with samples from the lowlands and highlands of Santa Cruz, Isabela, and Floreana (Dudaniec et al. 2008). Landscape genetic analyses detected two distinct genetic clusters, flies from Isabela and Santa Cruz forming one, and Floreana flies forming the other. There was no differentiation within any island, suggesting either high levels of fly dispersal, not enough time since arrival and establishment within the archipelago, or both. The most conservative conclusion is that the fly has a high dispersal capacity and poses a serious threat to the reproductive success of Galapagos passerine birds. Additionally, *P. downsi* may be moved around between islands by humans, which increases the risk of spread (*see* Sect. 8.9).

Studies of ectoparasites on Galapagos animals are useful for understanding parasite spread and, in some cases, helpful for elucidating patterns of host population connectivity. Whiteman et al. (2007) studied three ectoparasites (two lice, *Degeeriella regalis* and *Colpocephalum turbinatum*, and one hippoboscid fly, *Icosta nigra*) that infect Galapagos hawks. These parasites differ in life history traits including dispersal ability, transmission mode, and life cycle. A population genetic study using mitochondrial DNA found that all three parasite species showed significant genetic differentiation across islands, and that the degree of structure was predicted by the ecology of each parasite species (Whiteman et al. 2007). The less mobile feather louse, *D. regalis*, had the most evident population genetic structure, while the body louse, *C. turbinatum*, had less, and the hippoboscid fly was the least differentiated of the three. This study and more recent work (Koop et al. 2014) demonstrate that the most host-associated parasites closely track their hosts, and because of shorter generation times and higher mutation rates, these parasites can provide more information on population differentiation and connectivity than host DNA alone can reveal.

A similar study of ectoparasites (two louse species, *Myrsidea nsomimi* and *Brueelia galapagoensis*, and one *Analges* mite) on Galapagos mockingbirds showed an overall pattern of strong phylogeographic congruence (Štefka et al. 2011). The mite species was the most genetically differentiated, with no shared haplotypes between islands. The opposite pattern was found in the feather louse, *B. galapagoensis*, which had low genetic variability and weak population differentiation that was not congruent with the patterns recovered in the mockingbird host (Štefka et al. 2011). Feather mites, lice, and hippoboscid flies tend to be host-specific and are not typically thought to harm their hosts (but see Whiteman et al. 2006b). Therefore, while we can learn a lot about parasite spread relative to parasite life history characteristics and host population connectivity from ectoparasites, they are not likely to spread to other host species (host switching and spillover is covered in Chaps. 6 and 7).

Salmonella enterica is a common bacterial pathogen that has been studied in Galapagos land and marine iguana populations (Franco et al. 2011; Wheeler et al. 2011; Lankau et al. 2012). Considerable sequence and serotype diversity was found, and strains tended to be more similar to others from the same sampling locale and, to a lesser extent, to those recovered from either marine or land iguanas (Wheeler et al. 2011). Some *S. enterica* strains are shared between marine and land iguanas, which is consistent with habitat overlap, especially on small islets like Plaza Sur, off the coast of Santa Cruz (Wheeler et al. 2011). A second study found similar results, with unique *S. enterica* assemblages per sampling location and no effect of host species (marine or land iguana) (Lankau et al. 2012). Lankau et al. (2012) also found that *S. enterica* variation was oriented along a southeast to northwest axis within the archipelago. Dispersal (and horizontal gene transmission) between *S. enterica* populations probably occurs rarely and only between proximate sites. This is consistent with the pattern of strong population genetic structure found in both marine and land iguanas (Table 8.1, MacLeod et al. 2015, Tzika et al. 2008).

8.7 General Patterns in Population Connectivity of Galapagos Hosts, Vectors, and Parasites

We have graphically compiled some of the known patterns of population differentiation for the terrestrial animals, vectors, and parasites in Galapagos (Fig. 8.3). Although the focus of the chapter is on parasite spread and the role of host movement, it is more straightforward to visually present the *lack of gene flow* and the inferred *lack of movement* than to clearly illustrate population connectivity. Therefore, we have listed the number of unique genetic clusters found on those islands (Fig. 8.3). We have not included animals that have diverged into separate species or subspecies on some, all, or nearly all of the islands where they are found (e.g., lava lizards (*Microlophus* spp.), giant tortoises, and mockingbirds). San Cristobal, Santa Cruz, Genovesa, Pinta, and Isabela + Fernandina each harbor unique genetic populations of five species. Española, Floreana, Fernandina, and Isabela each have four species with unique genetic composition compared to the rest of the archipelago (Fig. 8.3). Santiago and Santa Fe have unique genetic populations for three species, and Marchena and a grouping of Darwin and Wolf combined, and a larger cluster of Isabela, Fernandina, and Santa Cruz each are associated with unique genetic clusters for two species (Fig. 8.3).

This graphic allows us to visualize genetic isolation within the archipelago. We did not include any unique species-specific patterns, so this figure overemphasizes the isolation. For example, Nazca boobies on Española and Genovesa comprise a

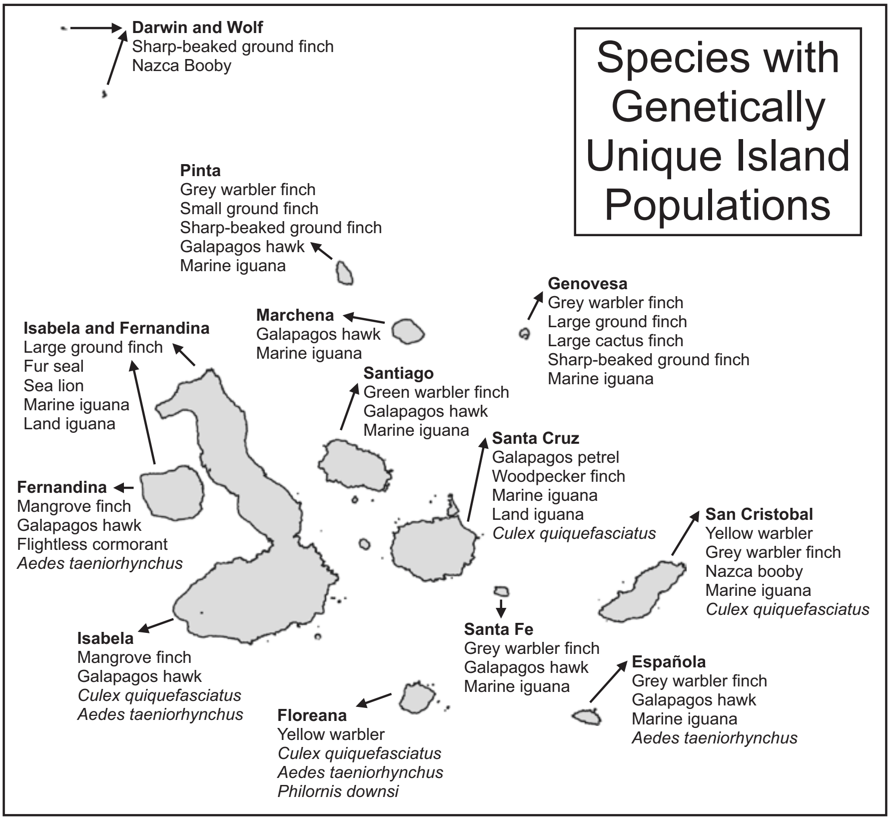

Fig. 8.3 General patterns of population genetic uniqueness within the Galapagos Islands. Lists show the species that have a genetically unique population on the associated island or island cluster. Clusters unique to particular species are not shown (e.g., genetic cluster comprised of Nazca boobies from Genovesa and Española) and differentiation at the subspecies and species level is not included

unique genetic cluster (Levin et al. 2013), but this cluster is not recovered in any other population genetic studies of Galapagos animals. Other larger genetic clusters are less likely to be shared between species, such as the large ground finch cluster on Pinta, Marchena, Santiago, Daphne, and Santa Cruz (Farrington et al. 2014) or the southern house mosquito cluster on part of Fernandina, Baltra, and the lowlands of San Cristobal, Santiago, and Santa Cruz (Bataille et al. 2009b). Sampling effort, sample size, and the type of molecular marker can also affect the population genetic patterns, making direct and quantitative comparison challenging. The general conclusion is that outlying islands, and older islands, tend to have larger numbers of species with unique genetic clusters and that there is more gene flow between the central "core" islands. For example, if a specialist parasite was introduced to San Cristobal, the risk of spread might be low if it infected one of the species that does not show evidence of movement between nearby islands. However, spread would be inevitable if the parasite was a generalist, or if it infected one of the animals that shows widespread movement throughout the archipelago.

8.8 Host-Parasite Co-Structure Studies: Two Examples from Galapagos

We have argued that understanding patterns of host (and vector) population connectivity is critical for predicting parasite spread. In a few cases, we have information on population connectivity for Galapagos hosts and their parasites. These co-structure studies provide important evidence that host population structure can predict parasite population structure, and can also reveal situations in which this is not the case. The closely host-associated feather louse, *D. regalis*, found on Galapagos hawks show patterns of population differentiation that almost perfectly mirror those recovered in the hawk (Koop et al. 2014; Fig. 8.4). This indicates that the louse populations track the hawk's evolutionary history and movements throughout the archipelago. In this case, the patterns in the host are a good predictor of parasite population connectivity and spread. On the other hand, host population genetic patterns may not always mirror parasite population structure. Hippoboscid fly (*O. spinifera, O. aenescens*) populations show no population genetic structure throughout the archipelago despite marked differences in differentiation in their hosts (Levin and Parker 2013; Fig. 8.4). There is little genetic exchange between several populations of Nazca boobies, and yet *O. aenescens* populations show high levels of gene flow, similar to pattern found in *O. spinifera*, which infect the panmictic Galapagos population of great frigatebirds (Fig. 8.4). Therefore, host population genetic patterns do not always predict patterns of parasite population connectivity. Knowledge of both enhances our understanding of the biology of both host and parasite. Because the flies infecting Nazca boobies appear to exchange genes when the birds do not, we assume that the birds move more readily between islands than previously thought, facilitating fly dispersal. Alternative explanations include occasional fly movement aboard an atypical host, or independent movement by the flies, which is currently unknown. Thus, understanding parasite population connectivity can strengthen our inference about host population connectivity, especially in cases where the host is highly vagile but extremely site philopatric, as with the Nazca booby.

8.9 Human-Facilitated Parasite Spread in Galapagos

Since their discovery of the Galapagos archipelago, humans have traveled across and between islands, potentially disturbing patterns of connectivity and movements of hosts and parasites alike. The capacity of humans to spread species and alter their population structure has never been as high as in the recent decades. Five islands are

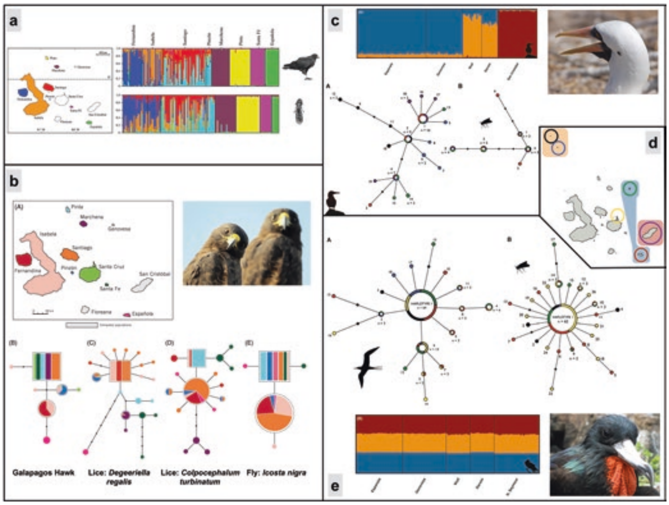

Fig. 8.4 Two examples of population genetic co-structure studies of Galapagos birds and their ectoparasites. (**a**) Genetic cluster assignment of Galapagos hawks (*Buteo galapagoensis*) (*top panel*) and *Degeeriella regalis* feather lice (*bottom panel*) by island using microsatellite markers. Lice closely track hawk hosts and both are generally distinct by island. Colors correspond to islands on map. Reprinted with permission from Koop et al. 2014. (**b**) Mitochondrial DNA (mtDNA) haplotype networks for Galapagos hawks and three ectoparasites. There is little mtDNA differentiation in the host; however, lice (*D. regalis* and *Colpocephalum turbinatum*) collected from hawks delineate island groups better than DNA from the host. Hippoboscid fly, *Icosta nigra*, has low genetic variation and no evident population genetic structure. Photo by J.M. Pogacnik. Reprinted with permission from Whiteman et al. 2007. (**c**) Genetic cluster assignment via microsatellite markers (panel) and mtDNA haplotype network for Nazca boobies (*Sula granti*) and mtDNA network for hippoboscid fly, *Olfersia aenescens,* in Galapagos. The host shows evidence of population genetic structure while the fly does not. Photo by I.I. Levin. (**d**) Map of Galapagos indicating sampling for Nazca boobies, great frigatebirds (*Fregata minor*) and their hippoboscid flies. *Colored* circles match colors in haplotype networks and shaded colors match unique genetic clusters identified in Nazca boobies in (**c**). (**e**) mtDNA haplotype network and genetic clustering output for great frigatebirds and mtDNA haplotype network for hippoboscid fly, *Olfersia spinifera*. No genetic structure exists in either host or parasite. Photo by I.I. Levin. (**c**) and (**e**) reprinted with permission from Levin and Parker 2013 or under a Creative Commons License. Photos reprinted with permission of photographers

now inhabited by over 25,000 residents, with ferries and planes connecting them several times a week. In 2011, more than 8700 ferries, and 1800 flights have made the journey between two islands (Galapagos quarantine and inspection system-SICGAL annual report 2011). In addition, cargo ships coming to San Cristobal Island from mainland Ecuador (more than 200 trips in 2011) also stop by Santa Cruz and Isabela Islands before going back to the mainland. A large part of the tourism industry also consists of boat cruises of 3–7 days hopping between various islands. There are now more than 80 tourist vessels in the archipelago serving over 170,000 tourists a year (Epler 2007, Galapagos quarantine and inspection system-SICGAL annual report 2011).

This human-induced inter-island connectivity has helped spread parasite-infected invasive species, such as chickens carrying multiple bacteria and viruses, cats with *Toxoplasma gondii*, or dogs with canine distemper (*see* Chap. 3 for a detailed list and references). Detection of inter-island gene flow in populations of the introduced ectoparasitic fly *Philornis downsi* and disease vector *Culex quinquefasciatus* also suggests that human movement likely helps the spread and movement of these species (Dudaniec et al. 2008; Bataille et al. 2009b). This is especially likely for *C. quinquefasciatus,* a mosquito with a flying capacity too poor to cross kilometers of sea unaided. This hypothesis is supported by a study that assessed attraction of insects by lights of tourist boats during the night (Roque Albelo et al. 2006). The authors sampled tourist boats for insects during multiple nights summing over 100 h of sampling, and collected over 2000 specimens of 171 different species (10 orders), including the disease vectors *A. taeniorhynchus* and *C. quinquefasciatus.*

Human movement may have also modified, or is currently modifying, some endemic host-parasite interactions. Some native fauna have been moved around by humans in the early days of Galapagos colonization. For example, whalers and buccaneers have moved tortoises between islands, changing their genetic make-up (Poulakakis et al. 2008, 2012), and probably their parasite assemblage (Fournié et al. 2015). Bataille et al. (2011) observed higher level of inter-island gene flow among *A. taeniorhynchus* populations collected near the major ports of the archipelago, providing further evidence that boats helped their movement between islands. Unfortunately, effects of these new disease vector migration patterns on host-parasite interactions have not been studied, but could be assessed with the help of phylogenetic studies. For example, a vector-borne parasite species with an island-specific lineage structure that reflects the poor dispersal capacity of its host may present a mixture of lineages unique to inhabited islands due to human-aided connectivity of its vector populations. Bataille et al. (2012) speculated that *A. taeniorhynchus* played this role of parasite lineage mixture for *Hepatozoon* blood parasites infecting Galapagos reptiles, although transmission of this parasite by mosquitoes typically occurs only if infected mosquitoes are ingested by the host (Telford et al. 2001). One final example of the potential role of humans in the spread of pathogens is that of the avian pox virus. Pox-like symptoms show up in museum collections of Galapagos birds in 1898/1899 localized in birds on San Cristobal, which had the largest human population at that time. These symptoms were confirmed through histopathology and genetics as pox. The same collections confirmed its spread shortly thereafter to southern Isabela, which had the second-highest human population (Parker et al. 2011). The pox virus is vectored mechanically by biting insects that pass virions directly from one blood-meal host to the next, or more passively by durable virions in the substrate that can be picked up by any object such as shoes.

Modification of Galapagos habitats due to human activities could also facilitate the spread of parasites. Most of Galapagos highland habitats on inhabited islands have been modified for agriculture. This fragmentation of the natural habitat of Galapagos endemic fauna may have increased the chance of contact with introduced species and their parasites, favoring their spread to native hosts (*see* Chap. 7 on host switching). Human activities may also have modified the population dynamics of endemic parasite and vector species. For example, agriculture has increased the access to fresh water in areas where this resource is normally scarce. The endemic mosquito *A. taeniorhynchus* does breed in highland habitats but highland populations are limited by breeding pools (Bataille et al. 2010). Agriculture has provided *A. taeniorhynchus* with new breeding sites, likely increasing its population and its connectivity with coastal populations, and its capacity to spread parasites across habitats.

8.10 Conclusion

Surprisingly little is known about parasite spread within the Galapagos Islands. However, there is a great deal of information on host and vector population connectivity, which we argue can inform our understanding of potential parasite spread. Co-structure studies, where population connectivity of host and parasite is simultaneously evaluated, are one of the best tools for understanding parasite spread, and this approach should be employed more in the future. Unfortunately, it can be very hard to contain the spread of a parasite if suitable host(s) and vector(s) are present. The increasing resident population and tourism activities in the Galapagos Islands greatly enhance the risk of parasite and vector spread across the islands, even for species with poor dispersal capacity. Therefore, our best approach to preventing parasite spread is to prevent the human-aided colonization of novel parasites, hosts, and vectors (*see* Chap. 3).

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Chapter 9

Invasion of an Avian Nest Parasite, *Philornis downsi*, to the Galapagos Islands: Colonization History, Adaptations to Novel Ecosystems, and Conservation Challenges

Birgit Fessl, George E. Heimpel, and Charlotte E. Causton

Abstract This chapter discusses the invasion of an avian nest fly, *Philornis downsi*, to the Galapagos Islands, its interactions with novel bird hosts, and the strategies that are being implemented to protect threatened, endemic bird species. *Philornis downsi* was first recorded in the Galapagos less than 60 years ago and is the first bird parasite with parasitic larval stages and non-parasitic adults to reach the islands. Since its introduction, it has successfully spread to most islands and habitats in the archipelago and is associated with a wide range of bird hosts. The consequences of its feeding habits on naive birds have been deleterious to a large number of species, many of which are in decline. An international research group, coordinated by the Charles Darwin Foundation and Galapagos National Park Directorate, is studying various aspects of the biology of *P. downsi* and its impacts on selected bird species with the aim of fully understanding the complex interactions between flies and birds. The ultimate aim of these investigations is the development of effective management tools.

Keywords Host range • Host-parasite interactions • Arms race • Darwin's Finches • Life history • Management

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9.1 Introduction

The successful colonization of a parasite in a novel environment involves a series of steps that often depend on the parasite's ability to adopt and adapt to novel hosts (both native and alien species) once it has arrived (Blackburn and Ewen 2016). Once established, parasite spread is reliant on parasites building up healthy populations on their hosts, but at a level that does not kill the host before the parasite life cycle is completed (Schmid-Hempel and Ebert 2003; Hatcher et al. 2012). Novel hosts with little or no experience with parasites, such as those found in island ecosystems, may be particularly vulnerable (Wikelski et al. 2004; Lymbery et al. 2014). Invasion success over the long term will depend on the evolutionary changes that take place between the parasite and hosts to adapt to this new relationship (Hatcher et al. 2012). This invasion scenario is the case for most endoparasites and ectoparasites, but is complicated by additional steps for parasites with life cycles that require the presence of vectors or intermediate hosts (Prenter et al. 2004; Lymbery et al. 2014). On the other hand, the invasion process is simplified for ectoparasites with free-living stages that are not dependent on a host for translocation. This chapter examines the case of an avian ectoparasite with a free-living adult stage, *Philornis downsi*, the processes underlying its colonization and establishment in the Galapagos Islands, its interactions with novel bird hosts, and conservation actions that are being undertaken to remediate impacts on populations of threatened, endemic bird species.

9.1.1 Background on the Genus Philornis

The New World genus *Philornis* (family Muscidae, order Diptera) contains approximately 50 described species (Couri et al. 2007). All species for which some ecological data are known complete their life cycle in bird nests, either as commensals with free-living larvae (two species) or as ectoparasites ingesting blood and fluid (two species including *P. downsi*), or as subcutaneous feeders on blood and tissue (18 species) (Teixeira 1999; Dudaniec and Kleindorfer 2006). All species are associated with altricial or semi-altricial birds, i.e., species whose nestlings stay in the nest for longer than 2 days and, at times, several *Philornis* species can be found in a given nest (Bulgarella et al. 2015, 2017). Studies on the effects of the genus *Philornis* on host species are still few in number, but they show that impacts vary depending on larval feeding niche, competition with other parasites and predators, parasite intensity, host body size and clutch size, and environmental factors (Young 1993; Arendt 2000; Antoniazzi et al. 2011; Segura and Reboreda 2011; Koop et al. 2013a; Knutie et al. 2016, 2017). *Philornis* shares many similarities with the old-world genus *Passeromyia* (family Muscidae) (five species including scavengers, blood-sucking ectoparasites, and subcutaneous parasites) (Couri and de Carvalho 2003) and the North American genus *Protocalliphora* (family Calliphoridae), with approximately 40 species, almost all of them avian ectoparasites (Sabrosky et al. 1989; Bennett and Whitworth 1991). Of all these avian nest parasites, *P. downsi* has received the greatest attention in the last 20 years with over 30 articles documenting and discussing its detrimental impacts on an array of bird species. Almost all of these studies have been conducted in the Galapagos Islands, the only location where it is known to be invasive.

9.1.2 **P. downsi** *in Galapagos*

Philornis downsi was first recorded in the Galapagos Islands less than 60 years ago and to our knowledge is the first ectoparasite of birds with free-living adults to have arrived in the islands in recent years (Sect. 9.2). Since its introduction, it has successfully colonized most islands and habitats in the archipelago and is associated with a wide range of hosts (Sect. 9.3). The consequences of its feeding habits on naive birds have been deleterious to a large number of species (Sects. 9.4 and 9.5). All immature stages of *P. downsi* feed on the blood of nestlings (Fig. 9.1), unlike adult flies that presumably feed mainly on plant exudates. Female flies lay their eggs in the base of bird nests, enabling newly emerged larvae to find hosts easily (O'Connor et al. 2010a; Lincango et al. 2015). On hatching, the first-instar larvae often migrate to feed in the nares and/or auditory canals of young nestlings, these areas providing a moist environment and easy access to fluids for young larvae (Fessl et al. 2006a). The second and third larval stages are typically found in the base of the nests and emerge during the night to feed on the blood of the nestlings. They might change to saprophagous feeding behavior if their host dies (Huber 2008; O’Connor et al. 2010a). Third-instar larvae then burrow into the nest bottom and pupate there, forming a frothy cocoon. The puparia or pupal cases remain in the nesting material and parasite intensity can be established by carefully dismantling the nest once activity has ceased. *Philornis downsi* parasitism is known to cause anemia—reduced hemoglobin levels and thus reduced oxygen transport, reduced nestling growth rates and increased nestling mortality, though values of different studies vary considerably (*see* Sect. 9.4).

Substantial gaps still exist in the understanding of the life history and ecology of *P. downsi*, and this information is needed for the development of techniques to effectively mitigate the effects of this parasite on endemic birds that are at risk (Sect. 9.6). An international research group, coordinated by the Charles Darwin Foundation (CDF) and Galapagos National Park Directorate (GNPD), is currently studying various aspects of *P. downsi* biology and its impacts on selected bird species in combination with other factors (e.g., rainfall, food availability, habitat management) with the aim of fully understanding the complex interactions between flies and birds and developing effective control techniques. A better understanding of its colonization history and its distribution and abundance in continental South America is also being sought to develop management plans for effectively preventing further introductions of this kind.

Fig. 9.1 Life cycle of *Philornis downsi*. Adults are free living, feeding on fruits and flowers. Females lay eggs in bird nests with eggs or chicks. First-instar larvae often move into nostrils, ear openings and feather quills. Second- and third-instar larvae remain in the nest bottom during the day and feed on nestling blood during the night. Pupation occurs in the nest bottom and parasite intensity can be determined by examining pupal cases in previously used bird nests. Source life cycle development times: Lincango et al. in prep. Lahuatte et al. 2016, Lincango and Causton 2008. Photos: H Herrera, J O'Connor, A Hendry

9.2 The Invasion of the Galapagos Islands by *P. downsi*

Here, we provide some background on *P. downsi* in its native range and consider the main hypotheses for its invasion of the Galapagos Islands. In particular, we ask how strong the evidence is for a human-aided invasion rather than a natural event and consider the potential colonization routes of a human-aided invasion.

9.2.1 P. downsi *in its Native Range*

The known natural geographic range of *P. downsi* includes Trinidad and Tobago (Dodge and Aitken 1968), Brazil (de Carvalho and Couri 1999), Argentina (Silvestri et al. 2010), and mainland Ecuador (Bulgarella et al. 2015). Given the difficulties in encountering *P. downsi* in the field and the paucity of *Philornis* researchers, it seems likely that the native range of this species contains other South America countries and possibly Central America, Mexico, and other Caribbean Islands in addition to Trinidad (though it is apparently absent from Tobago; Knutie et al. 2017). To find *P. downsi* in the field, bird nests have to be examined, but even then the free-living and nocturnal nature of larval feeding makes them easy to be overlooked; most other *Philornis* species are noticeable to investigators handling bird nestlings due to the large subcutaneous larvae. Studies in the native range have revealed a relatively broad range of host associations that appears to be centered on the order Passeriformes, although some members of the Piciformes (woodpeckers and allies), and Cuculiformes (cuckoos and allies) are attacked as well (Dodge and Aitken 1968, de Carvalho and Couri 1999, Teixeira 1999, Silvestri et al. 2010, Bulgarella et al. 2015) (Table 9.1). As with the geographical range, the known host range is likely an underestimate due to the difficulty of encountering *P. downsi*.

Despite these difficulties, some information on *Philornis*-host associations in the native range is available. The best data set comes from the island of Trinidad, where Dodge and Aitken (1968) investigated 29 bird species over a 12-year period in the 1950s and 1960s, finding 10 *Philornis* species associated with birds. These data were re-analyzed by Bulgarella and Heimpel (2015). Of the 29 bird species investigated, *P. downsi* attacked 16 (Fig. 9.2). As noted above, most of these were in the Passeriformes (14) but one was in the Piciformes—the Rufous-tailed Jacamar (*Galbula ruficauda*) and one was in the Cuculiformes—the Smooth-billed Ani (*Crotophaga ani*). Of the 10 *Philornis* species observed, *P. downsi* was associated with the largest number of bird species. However, many of the bird species in the data set did not exhibit *P. downsi* parasitism. These included birds in various orders, including the Psittaciformes (parrots), Strigiformes (owls), Columbiformes (pigeons and doves), and Apodiformes (hummingbirds).

The Galapagos Islands supports a high abundance and moderate diversity of Passeriformes, and this likely facilitated the invasion of *P. downsi* into Galapagos.

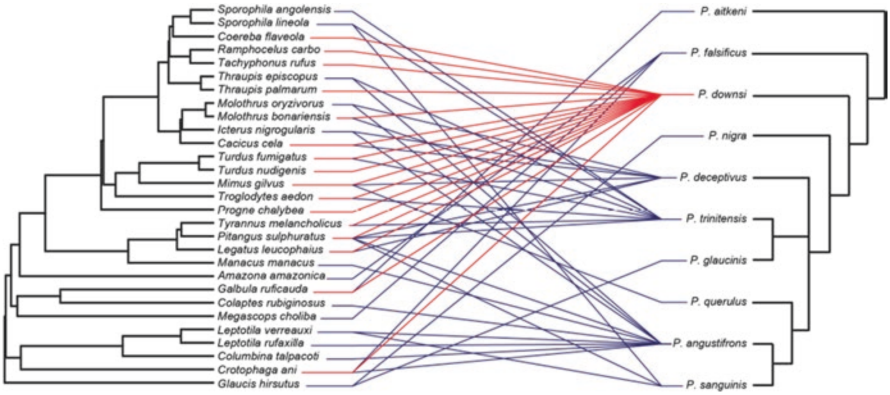

Fig. 9.2 Phylograms of birds (*left*) and *Philornis* spp. (*right*) and lines indicating bird/*Philornis* associations in Trinidad as observed in the 1950s and 1960s by Dodge and Aitken (1968). Each line signifies at least one rearing record. Figure taken from Bulgarella and Heimpel (2015)

Table 9.1 Bird species (with order and family) known to be infested by *P. downsi* throughout its native and introduced ranges

Order	Family	Bird species	Common name	Reference (first record only)	Geographic region: Island
Cuculiformes	Cuculidae	*Coccyzus melacoryphus*	Dark-billed Cuckoo	Fessl et al. (2001)	Galapagos: Santa Cruz
		Crotophaga ani	Smooth-billed Ani	Dodge and Aitken (1968); Fessl et al. (2001)	Trinidad; Galapagos: Santa Cruz, Isabela
Passeriformes	Coerebidae	*Coereba flaveola*	Bananaquit	Dodge and Aitken (1968)	Trinidad
	Dendrocolaptidae	*Lepidocolaptes souleyetii*	Streak-headed Woodcreeper	Bulgarella et al. (2015)	Mainland Ecuador
	Emberizidae	*Zonotrichia capensis*	Rufous-collared Sparrow	Teixeira (1999)	Unknown
	Estrildidae	*Lonchura domestica*	Society Finch	Bulgarella et al. (2017)	Caged birds, USA
		Taeniopygia guttata	Zebra Finch	Heimpel et al. unpublished	Caged birds, USA
	Hirundinidae	*Progne chalybea*	Gray-breasted Martin	Dodge and Aitken 1968	Trinidad
	Icteridae	*Cacicus cela*	Yellow-rumped Cacique	Dodge and Aitken (1968); Bulgarella et al. (2015)	Trinidad; mainland Ecuador
		Molothrus bonariensis	Shiny Cowbird	Dodge and Aitken (1968)	Trinidad
	Mimidae	*Mimus gilvus*	Tropical Mockingbird	Dodge and Aitken (1968)	Trinidad
		Mimus melanotis	**San Cristobal Mockingbird**	Causton et al. (2013)	Galapagos: San Cristóbal
		Mimus parvulus	**Galapagos Mockingbird**	Fessl et al. (2001)	Galapagos: Santa Cruz
		Mimus trifasciatus	**Floreana Mockingbird**	Wiedenfeld et al. (2007)	Galapagos: Floreana islets
	Parulidae	*Setophaga pitiayumi*	Tropical Parula	Bulgarella et al. (2017)	Mainland Ecuador
		Setophaga petechia	Yellow Warbler	Fessl et al. (2001)	Galapagos: Isabela, Santa Cruz
	Polyoptilidae	*Polioptila plumbea*	Tropical Gnatcatcher	Bulgarella et al. (2017)	Mainland Ecuador

	Thamnophilidae	*Thamnophilus ruficapillus*	Rufous-capped Antshrike	de Carvalho and Couri (1999)	Brazil
	Thraupidae	***Camarhynchus pallidus***	**Woodpecker Finch**	Fessl et al. (2001)	Galapagos: Santa Cruz
		Camarhynchus parvulus	**Small Tree-finch**	Fessl et al. (2001)	Galapagos: Floreana, Isabela, Santa Cruz
		Camarhynchus psittacula	**Large Tree-finch**	Fessl et al. (2001)	Galapagos: Santa Cruz
		Camarhynchus heliobates	**Mangrove Finch**	Fessl et al. (2010)	Galapagos: Isabela
		Camarhynchus pauper	**Medium Tree-finch**	O'Connor et al. (2010c)	Galapagos: Floreana
		Certhidea olivacea	**Green Warbler-finch**	Fessl et al. (2001)	Galapagos: Isabela, Santa Cruz
		Geospiza fortis	**Medium Ground-finch**	Fessl et al. (2001)	Galapagos: Isabela, San Cristóbal, Santa Cruz
		Geospiza fuliginosa	**Small Ground-finch**	Fessl et al. (2001)	Galapagos: Floreana, Isabela, San Cristóbal, Santa Cruz
		Geospiza magnirostris	**Large Ground-finch**	Causton et al. (2013)	Galapagos: Santa Cruz
		Geospiza scandens	**Common Cactus-finch**	Fessl and Tebbich (2002)	Galapagos: San Cristóbal, Santa Cruz
		Platyspiza crassirostris	**Vegetarian Finch**	Heimpel et al. (2017)	Galapagos: Santa Cruz

(continued)

Table 9.1 (continued)

Order	Family	Bird species	Common name	Reference (first record only)	Geographic region: Island
		Ramphocelus carbo	Silver-beaked Tanager	Dodge and Aitken (1968)	Trinidad
		Sicalis flaveola	Saffron Finch	Silvestri et al. (2011); M Torres unpublished	Argentina; mainland Ecuador
		Tachyphonus rufus	White-lined Tanager	Dodge and Aitken (1968)	Trinidad
		Thraupis palmarum	Palm Tanager	Dodge and Aitken (1968)	Trinidad
	Troglodytidae	*Campylorhynchus fasciatus*	Fasciated Wren	Bulgarella et al. (2015)	Mainland Ecuador
		Troglodytes aedon	House Wren	Dodge and Aitken (1968); Bulgarella et al. (2015)	Trinidad; mainland Ecuador
	Turdidae	*Turdus fumigatus*	Cocoa Thrush	Dodge and Aitken (1968)	Trinidad
		Turdus maculirostris	Ecuadorian Thrush	G Brito Vera unpublished	Mainland Ecuador
		Turdus nudigenis	Spectacled Thrush	Dodge and Aitken (1968)	Trinidad
	Tyrannidae	*Legatus leucophaius*	Piratic Flycatcher	Dodge and Aitken (1968)	Trinidad
		Myiarchus magnirostris	**Large-billed Flycatcher**	Fessl et al. (2006b)	Galapagos: Santa Cruz
		Myiarchus phaeocephalus	Sooty-crowned Flycatcher	G Brito Vera 2015 unpublished	Mainland Ecuador
		Pitangus sulphuratus	Great Kiskadee	Dodge and Aitken (1968)	Trinidad
		Pyrocephalus nanus	**Little Vermilion Flycatcher**	Fessl and Tebbich (2002)	Galapagos: Isabela, Santa Cruz
		Tyrannus melancholicus	Tropical Kingbird	Dodge and Aitken (1968)	Trinidad
Piciformes	Galbulidae	*Galbula ruficauda*	Rufous-tailed Jacamar	Dodge and Aitken (1968)	Trinidad

Endemic Galapagos taxa have common names in *bold* and Latin names in *bold* if IUCN status is *threatened*

Nearly all of the passerines in Galapagos have been recorded as hosts (*see* Table 9.1, Sect. 9.3.3) with the remaining species likely not recorded as hosts due to insufficient sampling or lack of geographical overlap. While all of the endemic passerine bird hosts in Galapagos are by definition novel hosts, it is no surprise that they have been attacked, given the pattern of host associations of this parasite in the native range.

9.2.2 Colonization of Galapagos by P. downsi

But how did *P. downsi* arrive in the Galapagos in the first place? The first record of this species in the islands is from 1964 (Causton et al. 2006), in the form of eight individuals collected at two sites in Santa Cruz Island (one lowland and one highland); these specimens are now housed at the California Academy of Sciences in San Francisco (Fig. 9.3). Further sampling revealed *P. downsi* adults on various islands in 1989, 1991, and 1992 (B. J. Sinclair, personal communication), but the significance of all these samples was only recognized retroactively after B. Fessl

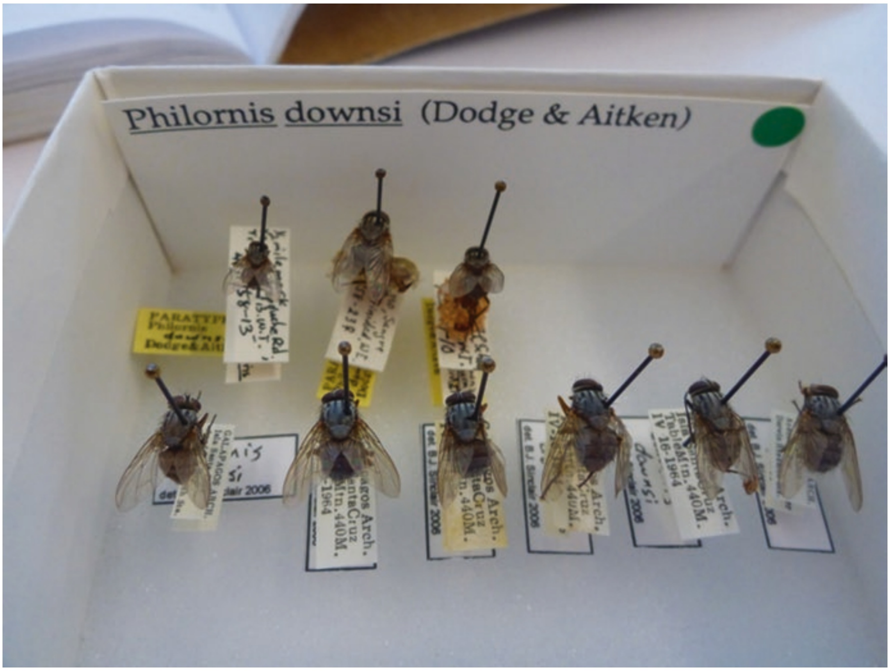

Fig. 9.3 The eight *Philornis downsi* individuals that were collected on Santa Cruz Island, Galapagos, and that are held at the California Academy of Sciences in San Francisco. These *P. downsi* were collected from lowland and highland sites in 1964 and were identified by BJ Sinclair. They represent the first confirmed incidence of *P. downsi* in Galapagos. Photo: GE Heimpel

discovered *P. downsi* larvae within a Woodpecker Finch (*Camarhynchus pallidus*) nest on Santa Cruz Island in 1997 (Fessl and Tebbich 2002). This gap between the first record of *P. downsi* on the islands and the first finding of larvae in a nest is somewhat puzzling, especially given the many studies focusing on Darwin's Finches (*see* below). This may reflect a period of relatively low abundance of the parasite (Crooks 2005) and/or insufficient examination of nests in areas where *P. downsi* was abundant. In any case, by 2003/2004, *P. downsi* was found attacking numerous land bird species on numerous Galapagos Islands in a survey conducted by Wiedenfeld et al. (2007). Of 14 islands checked, 12 were found to support *P. downsi*; the exceptions were Española and Genovesa (Fig. 9.4). Since this survey, *P. downsi* has been found on an additional three islands: Daphne Major (Fessl et al. 2017), North Seymour (S. McNew, personal communication), and Baltra (W. Iñiguez, personal communication). We attempt here to address two questions regarding the invasion of *P. downsi* that have remained elusive: first, what is the evidence that the presence of *P. downsi* in Galapagos is the result of a human-aided invasion; and second, what is the most likely route and timing of invasion?

9.2.2.1 Human-Aided Invasion or Natural Event?

The colonization history of *P. downsi* in the Galapagos Islands is not well understood, but a number of lines of reasoning are consistent with a human-aided introduction rather than a natural dispersal event. No collections of insects on the islands prior to the one reported above reported this species (Linsley and Usinger 1966; Causton et al. 2006) and neither have any reports of parasitism been associated with inspections of finch nests prior to 1997 (Beebe 1924; Lack 1947; Grant 1986). This suggests a recent invasion during the time of human habitation, and so points to the involvement of humans in the arrival of *P. downsi*. Still, while it would perhaps be remarkable that such an important parasite would be missed by eminent scientists studying such an iconic group of birds, it must be noted that the number of finch nests and nestlings actually investigated prior to 1997 on islands now known to harbor *P. downsi* appears to have been quite small. Thus, while Boag and Grant (1984) weighed and banded nestlings from 670 finch nests in the 1970s and did not notice any sign of *Philornis*-like parasitism (P.T. Boag, personal communication), all of these observations were done on Daphne Major, which is not known to support a permanent population of *P. downsi* (*see* Sect. 9.3.6). Much smaller numbers of nests were investigated on Genovesa and Wolf (both not known to harbor *P. downsi*) and Marchena (known to harbor *P. downsi*, but only six nests are known to have been investigated) (Grant 1981, 1986).Investigations of nests and nestlings by Beebe (1924) and Lack (1947) took place as well but are not quantified.

Given the intense scrutiny of the beaks of Darwin's Finches over the last 80 years (Lack 1947; Grant and Grant 2008), the lack of reports of beak malformations consistent with *P. downsi* perhaps represents a stronger line of evidence for a recent invasion. The feeding of *P. downsi* larvae within host nares during early development can cause intense scarring and malformations, some of which likely carry over into the adult stage (Galligan and Kleindorfer 2009; Kleindorfer and Sulloway 2016). It is hard to

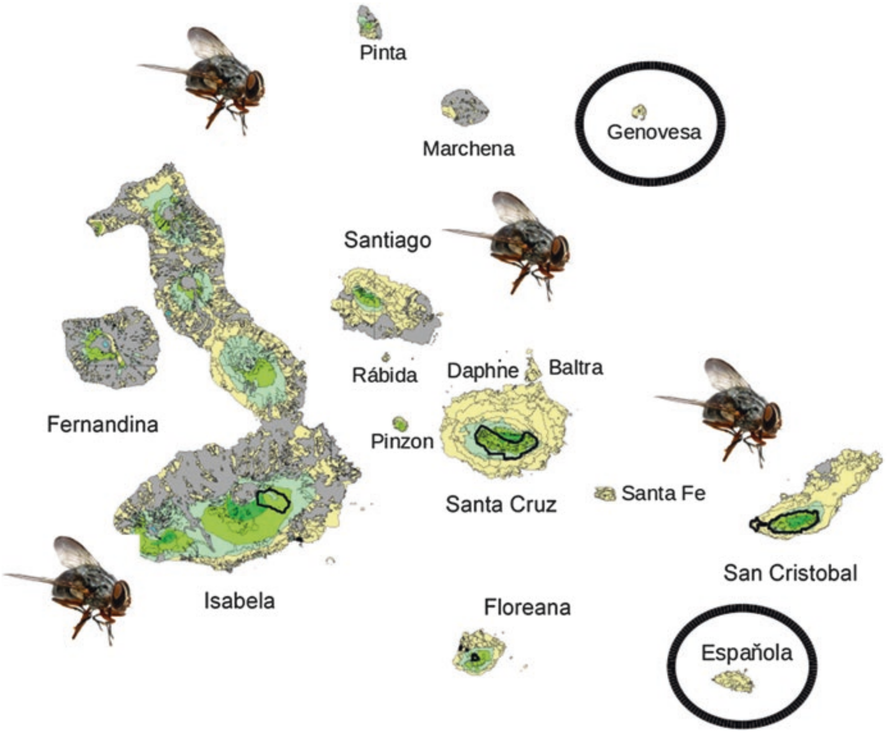

Fig. 9.4 *P. downsi* records from Galapagos. The only islands without flies are Genovesa and Espaňola. *P. downsi* has not been recorded from the northernmost Darwin and Wolf (not shown in map). Agricultural zones on inhabited islands are indicated by *black lines*, colors indicate different habitat zones: open lava (*grey*), dry zone vegetation (*light yellow*), transition zone (*bluish*), humid zone (*light green*), very humid zone (*green*), lagoon (*blue*)

believe that such scarring would have been overlooked in studies of finch populations with a high incidence of *P. downsi*. Here again, though, much of the work was done on islands such as Daphne Major and Genovesa that do not appear to harbor permanent populations of *P. downsi* (*see* Sect. 9.3). An approach investigating museum specimens for beak scarring could be fruitful to inform this hypothesis (Fig. 9.5), and indeed a recent study of museum specimens of the Small Ground-finch (*Geospiza fuliginosa*) on Floreana found that naris size consistent with beak scarring occurred only after 1960 (Kleindorfer and Sulloway 2016).

Other lines of reasoning support the hypothesis of a recent invasion. Dudaniec et al. (2008) performed a population genetics study incorporating eight microsatellite DNA markers and uncovered a significant heterozygote excess, which is consistent with a genetic bottleneck and thus bolsters the hypothesis that an invasion occurred. However, this analysis cannot properly distinguish between a recent human-aided introduction and a relatively recent natural dispersal event and it did not make any comparisons between *P. downsi* from Galapagos and from the native range. Bulgarella et al. (2015) performed such a comparison by sequencing a noncoding region of ribosomal DNA (ITS2) and found virtually identical sequences in samples collected

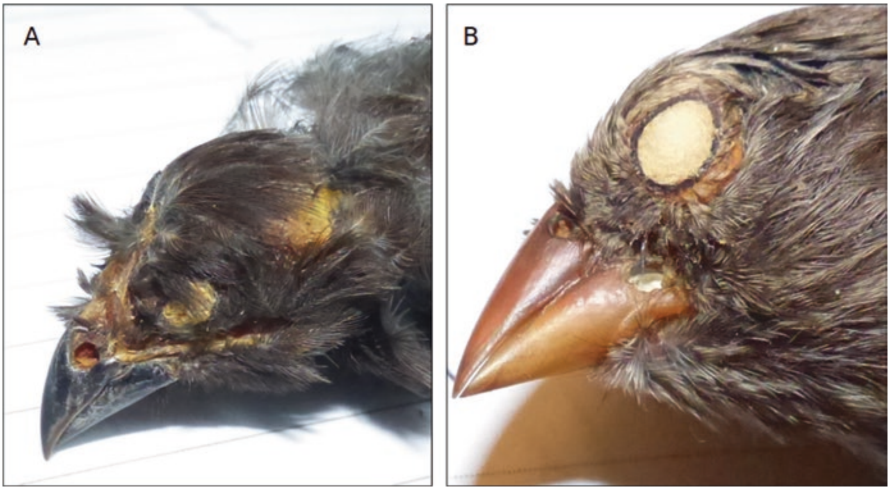

Fig. 9.5 (**a**) Photograph showing the left naris of an adult Small Ground-finch (*Geospiza fuliginosa*) collected on Santa Cruz Island, Galapagos in 1977 and curated at the Charles Darwin Research Station in Puerto Ayora, Santa Cruz Island, Galapagos. The naris opening is much larger and more round than a typical Small Ground-finch naris, shown in (**b**). The shape of the naris in (**a**) is similar in appearance to damage caused by *P. downsi* in nestlings (*see* Fig. 9.1) and may represent residual scarring in an adult bird that was caused by *P. downsi* feeding during the nestling stage. Photos: GE Heimpel

in Galapagos and mainland Ecuador. The same conclusion was drawn from an extension of this analysis incorporating sequences from two additional gene fragments (M. Bulgarella and G.E. Heimpel unpublished). This pattern is consistent with a recent invasion of the Galapagos but cannot be seen as conclusive support for the human-aided invasion hypothesis either.

Another line of evidence involves ecological patterns of abundance. A number of investigations of *Philornis* species infesting bird nests at field sites in mainland South America have found levels of parasitism that are substantially lower than that caused by *P. downsi* in Galapagos. This includes studies of *Philornis* species other than *downsi* (Young 1993; Nores 1995; Couri et al. 2005; Rabuffetti and Reboreda 2007; Antoniazzi et al. 2011; Quiroga and Reboreda 2012) and a recent study of *P. downsi* itself in mainland Ecuador (Bulgarella et al. 2015). This latter study showed that *P. downsi* was found in fewer than 30% of bird nests over two field sites and that the average number of *P. downsi* per infested nest was fewer than ten. This contrasts sharply with levels of parasitism in the Galapagos, where it is common for greater than 90% of nests in a given sample to be infested with *P. downsi* and for the average number of *P. downsi* larvae per nest to exceed 30 (sometimes greatly so) (*see* Sect. 9.4; Table 9.2).

Higher prevalence and per-nest abundance of *P. downsi* in Galapagos versus mainland Ecuador is consistent with a recent invasion. Two main hypotheses could explain such a pattern. The first is the enemy release hypothesis which posits that species experience enhanced abundance in their invaded range due to the absence of natural enemies that are present in the native range (Keane and Crawley 2002; Engelkes and Mills 2011). The level of parasitoid attack of *P. downsi* is much higher in mainland Ecuador than it is in Galapagos (Bulgarella et al. 2015, 2017), where it is negligible (M. P. Lincango, unpublished, see also the next section). Knutie et al. (2017) also found a relatively high rate of parasitism of *P. trinitensis* in Tobago by the recently discovered chalcidid parasitoid *Brachymeria philornisae* (Delvare et al. 2017). The second main hypothesis explaining higher parasitism rates in the introduced range of the parasites is the host defense hypothesis, which posits that naive hosts in introduced areas are less able to defend themselves against a novel parasite. Knutie et al. (2016, 2017) assessed this hypothesis by comparing the effects of *P. downsi* and *P. trinitensis* on closely related bird species in Galapagos and Tobago respectively. These studies showed similar patterns of response on the two islands and thus did not support the host defense hypothesis (Knutie et al. 2017). Rather, these authors concluded that enemy release from parasitoid (and possibly ant) attack was a more likely explanation for the higher prevalence and abundance of *Philornis* attack in Galapagos than in the native range.

9.2.2.2 Potential Routes of Invasion

We next consider the question of potential human-aided invasion routes to Galapagos for *P. downsi*. Hickman (1985) provided a review of human activities in the Galapagos Islands and his timeline reveals a number of potential invasion routes dating back to the 1300s when pre-Incan and then Incan seafarers are suspected of having reached Galapagos from the coast of Peru. A series of well-known visits to the islands follow, beginning with the accidental journey of Tomás de Berlanga from Panama in 1535 and including the voyage of the Beagle in 1835. To these must be added the use of the islands by pirates in the 17th and 18th centuries and whalers in the first half of the nineteenth century. More visits from Ecuador were associated with the annexation of Galapagos as a province of Ecuador in 1832. The early twentieth century saw a number of attempts at settlements that involved an increase in traffic between the mainland and the islands, and in the 1940s the US Army established a Naval Base on Baltra Island for 5 years. Tourism on the islands began in 1962 and has increased steadily until the present time. Along with increased tourism, medium-sized towns were established on Santa Cruz, San Cristóbal, and Isabela islands (and to a lesser extent Floreana). By the beginning of the twenty-first century, cargo ships and airplanes made the trip from Guayaquil on a regular basis and the frequency of these trips has increased steadily (Cruz and Causton 2007; Cruz Martinéz et al. 2007).

Transport by plane or ship during any of these periods constitutes a potential invasion route, with adult flies (like many other insects) hitchhiking in holds, decks, or cabins (Causton 2007; Causton et al. 2008; Herrera 2011), or possibly associated with fruit or other food cargo since adult *P. downsi* feed on soft tissues and juices of various fruits (Lahuatte et al. 2016). It is also conceivable that birds could nest within ship rigging while docked in the mainland and thus transport immature *P. downsi* to Galapagos given the correct timing. Current sanitary practices on boats from Guayaquil have likely reduced the risk of transport of insects from Guayaquil (G.E. Heimpel and M. Quiroga, personal observation in 2015) and planes are now routinely sprayed with insecticide to prevent new incursions, though occasional hitchhikers are still found (R. Azuero, personal communication). However, a likely period of optimal conditions for *P. downsi* introduction includes the early decades of the tourist period, as transport ships carrying food were increasing in frequency but sanitary methods had not yet been fully established.

Another possibility is that *P. downsi* was introduced along with introduced bird hosts. Pigeons were introduced into Galapagos in the early 1970s (Harmon et al. 1987) and one hypothesis could be that *P. downsi* was co-introduced with them (Wiedenfeld et al. 2007). However, as we have noted above there is no record of *P. downsi* attacking any member of the Columbiformes (*see* Table 9.1), so we deem this to be an unlikely route. Another potential co-introduction involves the Smooth-billed Ani (*Crotophaga ani*), which is known as a host for *P. downsi* in both the native range and Galapagos. Ranchers in Galapagos imported Anis in the 1960s in the mistaken belief that they would feed on cattle ticks (Rosenberg et al. 1990). While the details of the introduction are not known, if any nesting material was brought it could have included live *P. downsi* pupae.

Recent studies have shown that species of *Philornis* other than *downsi* are present in western Ecuador, including locations very close to Guayaquil (Bulgarella et al. 2015, 2017) (Fig. 9.6). Since all of these species are bird parasites, this

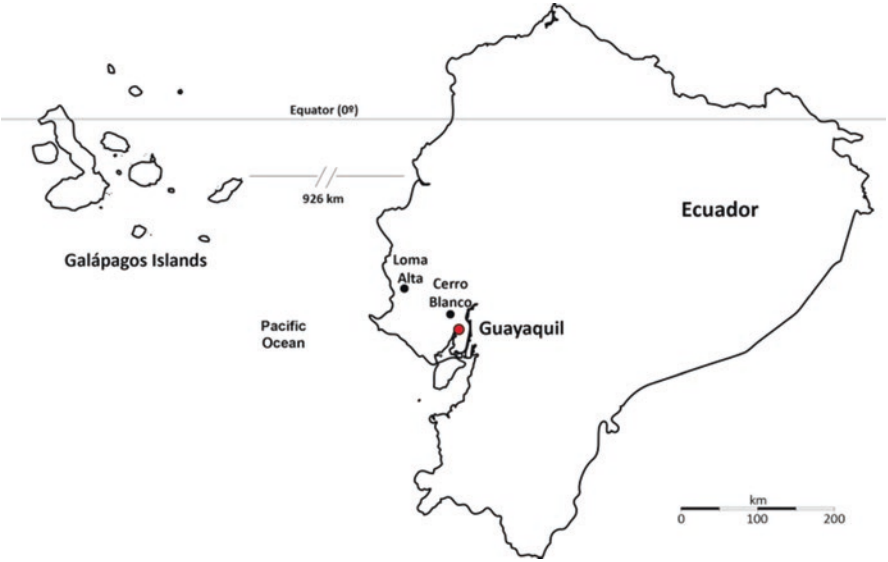

Fig. 9.6 A map of Ecuador showing the mainland sites where *P. downsi* has been found parasitizing various bird species. Cerro Blanco is the 'Bosque Protector Cerro Blanco', a tropical dry forest reserve within 10 km of the port city Guayaquil, and Loma Alta is the 'Reserva Ecologica Loma Alta', a transitional dry and premontane cloud forest reserve in Santa Elena province. Both sites exhibit a seasonal climatic pattern similar to that found in Galapagos. Adapted from Bulgarella et al. (2015) with permission

highlights the need to strengthen and enforce measures to exclude insects from ship and plane transport from mainland Ecuador to Galapagos.

9.3 What Makes *P. downsi* such a Successful Invader?

The probability of an insect species becoming invasive depends not only on its characteristics, but also on interactions with its new environment and stochastic events, e.g., available niches, disturbance, or climatic change (Heger and Trepl 2003; Crooks 2005; Jeschke et al. 2012). Characteristics associated with successful invading insects include polyphagy, a high competitive ability, a high intrinsic rate of increase, and an ability to inhabit a wide range of ecosystems (Crawley 1986, 1989; Lawton et al. 1986; Sakai et al. 2001; Engelkes and Mills 2011; Jarošík et al. 2015). Environmental factors that facilitate colonization include resource availability, the absence of natural enemies and competitors, and a suitable climate and habitat (Peterson 2003; Liebhold and Tobin 2008; Prior et al. 2015; Hui et al. 2016). Lastly, strong evidence exists to show that the greater the number of individuals introduced at a given time (propagule size) and the frequency of the introductions (propagule pressure), the greater genetic diversity and potential for adaptation to a novel environment. This, in combination with environmental suitability, will ultimately influence establishment and spread (Hayes and Barry 2008; Simberloff 2009; Duncan 2016; Garnas et al. 2016).

In this section, we consider some of the hypotheses that could explain the successful invasion of the Galapagos Islands by *P. downsi*. These include a broad feeding range, an absence of competition, strong dispersal capacity, wide climatic tolerance, and release from natural enemies.

9.3.1 Polyphagy of Adult Flies

Adult *P. downsi* feed mainly from fresh and decomposing flowers and fruits (Fig. 9.7). Field and laboratory studies suggest that they feed on a wide range of indigenous and introduced plant species including the invasive blackberry (*Rubus niveus*) (P. Lahuatte, unpublished) that is found in the humid highlands of inhabited islands. Polyphagous feeding habits by adults likely facilitated colonization of new areas and survival during the dry season when flowers and fruits are scarce (Heleno et al. 2013). Little is still known about what else *P. downsi* adults feed on or the range of plant species that they utilize, but studies on pollination networks suggest that it is not considered a major pollinator or a competitor of native pollinating species (Traveset et al. 2013, A. Traveset personal communication).

Fig. 9.7 *P. downsi* flies feeding on endemic *Tournefortia* sp. in the lowland arid zone on Santa Cruz Island, Galapagos. Photo D Cedeño

9.3.2 Reproductive Strategies

Multiple females lay eggs in nests irrespective of whether there are conspecific eggs or larvae in the nest already, and up to 200 eggs have been found in a single nest (Dudaniec et al. 2010; Lincango et al. 2015). This may be a strategy for survival when host numbers are low, and could increase the chances of flies finding a mate (Kleindorfer and Dudaniec 2009). Furthermore, by laying eggs in multiple nests of different host species, especially when nests are close together, *P. downsi* females can ensure that their offspring are distributed in a number of nests within a relatively short time frame, increasing the chances that progeny survive from some nests even if others are eliminated from factors such as climate extremes or predation (Kleindorfer and Dudaniec 2009; Dudaniec et al. 2010). The largest number of eggs laid by an individual *P. downsi* female in the laboratory has been 182 (P. Lincango, personal communication) and a genetic analysis suggests that females lay on average five eggs per nest with a maximum known estimate of 24 eggs per nest (Dudaniec et al. 2010). Given this, it is possible that a female could oviposit in 8–32 nests, guaranteeing multiple nests with progeny over its lifetime. From the perspective of the parasite, it may be advantageous to lay relatively few eggs in each nest to minimize risks of the host dying (Koop et al. 2013b; Kleindorfer et al. 2014).

9.3.3 Broad Host Range

The broad host range of *P. downsi* (Fig. 9.2, Table 9.1) has enabled it to establish new host-parasite relationships in Galapagos, despite the fact that it was probably introduced without any of its mainland hosts (*see* Sect. 9.2). Similar to its native range, the small-bodied passerines of the Galapagos Islands are hosts to *P. downsi* and include 11 of the 17 species of finch, 3 of the 4 mockingbirds, the Vermilion and Galapagos flycatchers, the Yellow Warbler (*Setophaga petechia*), the Dark-billed Cuckoo (*Coccyzus melacoryphus)*, and the introduced Smooth-billed Ani (Cuculidae) (Table 9.1, Fig. 9.8). It is likely that the remaining passerines that overlap with *P. downsi* geographically are also hosts. These include the Sharp-beaked Ground-finch (*Geospiza difficilis*), the Grey Warbler-finch (*Certhidea fusca*), and the IUCN Vulnerable Galapagos Martin (*Progne modesta*). Only passerines found exclusively on islands that are as yet free of *Philornis* are likely unaffected by this parasite: Genovesa Cactus-finch (*G. propingua*), Genovesa Ground-finch (*G. acutirostris*), Española Ground-finch (*G. conirostris*), Española Mockingbird (*Mimus macdonaldi*), and the Vampire Ground-finch (*G. septentrionalis*) found on Darwin and Wolf with unlikely *P. downsi* presence (*see* below).

9.3.4 Absence of Competitors

Adaptation to new hosts by *P. downsi* may have been facilitated in part by the absence of native competitors. To our knowledge, none of the ectoparasites found on small landbirds in Galapagos have life cycles that are similar to that of *P. downsi*. Most of the ectoparasites of Galapagos birds are either chewing lice (Insecta: Phthiraptera) or feather mites (Acari: Astigmata) that are commensal feeders on feathers, skin particles, and secretions (Sari et al. 2012; Palma and Peck 2013; Koop et al. 2014; Bulgarella and Palma 2017). Hippoboscid flies, otherwise known as “louse flies,” are the closest to *P. downsi* in terms of life history, but there is little evidence of ecological overlap. There are no reports of *P. downsi* being found on the same host individual as a hippoboscid fly, and even if this were to happen, overlap would be limited to the later stages of nestling development because adult hippoboscid flies (the only stage that feeds on the host) are most commonly found under feathers (Wood 2010; Waite et al. 2012). To date, two species of hippoboscids have been recorded on eight species of small landbirds in Galapagos (Harmon et al. 1987, B. J. Sinclair, unpublished); however, this group has not been adequately surveyed (Parker et al. 2006).

9.3.5 Strong Dispersal Capacity

P. downsi appear to be strong fliers based upon observations that they cross large lava fields (see below) but it is not clear whether they have dispersed between all islands in the archipelago independently or whether this dispersal has been aided by

Fig. 9.8 (**a**) Dome-shaped nests of Common Cactus-finch made out of dry grass and herbs in arid zone of Isabela Island and (**b**) of Small Tree-finch made out of twigs, moss and lichen in the Scalesia forest, Santa Cruz. (**c**) Cup nest of Galapagos Mockingbird made of dry Acacia sticks and branches in the arid zone of Santa Cruz and (**d**) of Vermilion Flycatcher made out of liverwort, little twigs and moss in the highlands of Isabela. Photos: A Cimadom (**a, b**), K Gotanda (**c**), D Mosquera (**d**)

humans. El Niño events (periods of heavy rain and strong winds) are associated with population growth and dispersal of terrestrial insects on the Galapagos Islands (Lubin 1985; Roque-Albelo and Causton 1999) and may have enabled spread. Boats may also have facilitated range expansion and increased the rate of introduction between islands. Tourist boats have played an important role in transporting insects between islands in the Galapagos archipelago, in particular Diptera and Lepidoptera (Roque-Albelo et al. 2006, 2008). Insects are attracted to certain lights on boats (Fig. 9.9) and many insects remain on board and are then transported to other islands. This includes *P. downsi,* which was tracked traveling from Baltra to Española and from Santa Cruz to Santiago islands (Lomas 2008). The risk of this happening has been reduced since the implementation of protocols to minimize the attraction of insects to lights on boats by the GNPD.

9.3.6 Climatic Adaptability

Philornis downsi is found on all the larger islands that support different vegetation zones as well as on some of the smaller (<20 km^2) islands with xerophilic vegetation only (Wiedenfeld et al. 2007) demonstrating adaptation to a wide variety of environments and climatic conditions. It has not been found on four islands on the northern or southerly edges of the archipelago. The two islands in the North, Darwin and Wolf, have not been surveyed, but are unlikely to be suitable year-round habitats for *P. downsi*. They are very small (<1.5 km^2) and are isolated from other landmasses by a minimum distance of 87 miles from other islands (Snell et al. 1996). Española and Genovesa are characterized by low elevations with arid zone vegetation (Fig. 9.10) and it may be that *P. downsi* flies have been unable to establish on these islands because they are farther away from other islands. Within-island surveys and studies on islands with different vegetation zones have found lower parasite incidence in nests at lower elevation, and in arid areas compared to the humid, higher elevation habitats (Wiedenfeld et al. 2007; O'Connor et al. 2010b). Dudaniec et al. (2007) did not find any differences in parasite intensity in different zones, but suggested that this may be a temporal effect and that numbers may depend on other factors such as the amount of rainfall, food availability for birds, and host density.

The abundance of *P. downsi* on the smaller, arid islands has yet to be monitored in a rigorous way to understand what drives population numbers. Very small islands (<1 km^2) do not appear to be suitable habitats for flies year-round and it is possible that these islands are only visited during times of high host abundance or favorable climate conditions. On Daphne Major, a small (0.32 km^2) island (Fig. 9.4) studied

Fig. 9.9 Insects attracted to the lights of a tourist boat. Some insects stay on boats and will be transported to the next island visited. Protocols to minimize the attraction of insects to lights on boats have been implemented by the GNPD. Photo: M Berg

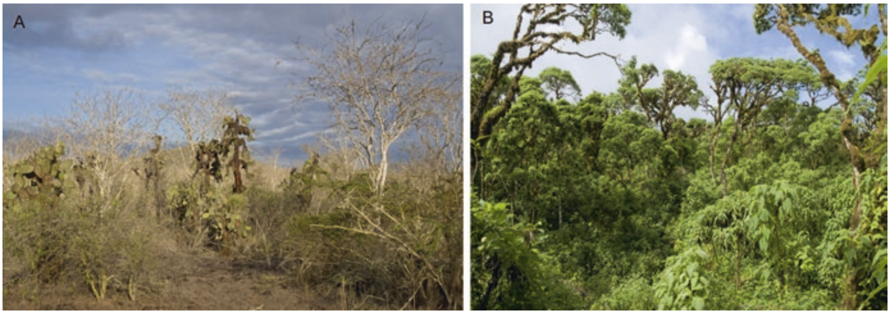

Fig. 9.10 (**a**) Typical arid zone vegetation with Cacti, Palo Santo and deciduous shrubs. (**b**) Humid highland forest consisting of the endemic *Scalesia pedunculata*. This habitat has been reduced and bigger forest patches now only exist on Santa Cruz and Floreana. Photos: M Dvorak, Santa Cruz

by P. and R. Grant for decades, *P. downsi* was first discovered in 2008 (Fessl et al. 2017). Regular checks by the Grants between 1997 and 2002 confirmed that nests were free of *Philornis* for at least 5 years, but nests were checked less intensively between 2002 and 2006 (P. and R. Grant, personal communication). Although it is possible that flies were present in low numbers during these interim years, heavy rainfall in 2008 (Trueman and d'Ozouville 2010) and higher numbers of nesting birds may have prompted spillover from Santa Cruz to neighboring islands.

Philornis downsi larvae also display tolerance for a range of micro-climatic conditions in Galapagos. Nests with larvae are found in most vegetational zones of the islands from mangrove forests to cooler, humid highlands and at elevations between sea level and 1050 m (Wiedenfeld et al. 2007, Mosquera et al. unpublished). Preliminary data from temperature sensors placed in nests suggest that despite the heat source provided by incubating females and young chicks, there are significant differences in nest temperatures between these locations. To date, *P. downsi* larvae have been found in nests with wide ranges of temperature (19–43 °C) and humidity (63–100% RH). Furthermore, nests of various types (Fig. 9.8) are parasitized ranging from open cup (Mockingbird, Dark-billed Cuckoo, Yellow Warbler, Vermilion Flycatcher (*Pyrocephalus nanus*)) to dome nests (Darwin's Finches) and secondary cavities (Galapagos Flycatcher (*Myiarchus magnirostris*)) as well as nests built of twigs in the arid zone (Mockingbird, Dark-billed Cuckoo, Smooth-billed Ani) to nests built of dense moss in the sometimes cool, humid highlands (some Darwin's Finches, Vermilion Flycatcher). *Philornis* have also been found in nest boxes that have been set up to study the Galapagos Flycatcher in Galapagos (D. Anchundia, unpublished) and other birds in mainland Ecuador (Bulgarella et al. 2015, 2017). To date, *P. downsi* has not been found in birds that nest on the ground but further investigations are required to determine whether it is exclusively arboreal.

In temporal terms, flies also show a capacity to survive unfavorable conditions. With a development time of approximately 22–24 days (Lahuatte et al. 2016) it is possible that at least three generations are produced during the main bird breeding season (January to April) which coincides with the rainy season in Galapagos (Grant 1986). For the rest of the year, bird nesting activity, and consequently host availability, is sporadic and patchy. This is especially the case in the arid zone, the largest vegetation zone in the archipelago. So what do flies do during this time and what strategies do they use to survive until the next breeding season? Evidence from a two-and-a-half year monitoring program has shown that female *P. downsi* are active throughout the year, including during the dry season (Causton et al., in prep.). This suggests that adult female flies are either able to survive until the onset of the main bird breeding season or that they utilize one or more of the very few host species that breed year-round to maintain populations. Many of the female *P. downsi* that are captured during the dry season have mated and carry a full load of eggs and thus would be ready to oviposit as soon as a host is found. Male flies, on the other hand, are not caught in traps during the latter part of the dry season, which suggests that they may be less resilient than their female counterparts, or use other survival strategies outside the nesting season (Causton et al., in prep.).

Philornis downsi demonstrate an ability to recuperate population numbers even after years with unfavorable climatic conditions. In Galapagos, drought years are associated with low bird breeding activity and low reproductive success (irrespective of whether nests are parasitized or not) (Grant 1986; Koop et al. 2013b). In the event that *P. downsi* is not using alternative hosts to passerines and Culiciformes, then host availability is considerably lower in these drought years (e.g., in Koop et al. 2013b for 2009), yet fly populations are able to bounce back in the following years (Koop et al. 2011; Knutie et al. 2013). It remains to be seen what would happen if drought conditions continued for several years. It is possible that *P. downsi* moves to areas where food and water are available (and there is possibly prolonged breeding of some hosts), such as in human settlements including agricultural zones. Little is known about fly movement, but evidence of flies migrating between forests separated by large (600 m) tracts of lava (F. Cunninghame, personal communication) suggest that flies are capable of dispersing over areas with harsh conditions.

9.3.7 Enemy Release

As noted above, the success of invasive species is often attributed to the absence of natural enemies in the introduced range (referred to as the enemy release hypothesis, *see* Keane and Crawley 2002 or Engelkes and Mills 2011). While 10–20% of *P. downsi* puparia are attacked by parasitoid wasps in mainland Ecuador (Bulgarella et al. 2015, 2017), and predation of larvae or pupae by ants may occur in the native range as well (Knutie et al. 2017; G.E. Heimpel unpublished), natural enemy attack in Galapagos appears to be virtually nonexistent. Although seven parasitoid species have been reared from *P. downsi* pupae in Galapagos (P. Lincango et al. unpublished), all are introduced generalists that produce very low levels of parasitism. The highest rate of parasitism was encountered in 2008 with 5% of nests containing at least one *P.*

downsi puparium attacked by one of two parasitoids species, *Spalangia endius* and *Brachymeria podagrica* (Lincango and Causton 2008). Both of these species are invasive in Galapagos and known to be generalist parasitoids of cyclorrhaphan fly pupae (Geden et al. 2006; Noyes 2017). This year was a particularly rainy year (Trueman and d'Ozouville 2010), which may account for the higher parasitism rates.

Evidence to date therefore suggests that *P. downsi* was not introduced with any important natural enemies (predators, parasitoids). However, it is still to be determined whether any other parasites, pathogens, or symbionts that are either beneficial, neutral, or detrimental to *P. downsi* have been co-introduced with it.

9.4 Host-Parasite Interactions—Evolution in Action?

In this section, we discuss the interactions between *P. downsi* and its hosts and discuss the prognosis for long-term fitness of both the hosts and the parasite. We also consider the hypothesis that *P. downsi* and its hosts in Galapagos are involved in the beginnings of an evolutionary “arms race” involving aspects of virulence on the part of *P. downsi* and aspects of resistance or tolerance on the part of the birds.

9.4.1 Effects of P. downsi *Parasitism*

Philornis infestations cause anemia in nestlings through reduced hemoglobin levels (Dudaniec et al. 2006; Fessl et al. 2006b; Knutie et al. 2016) and blood loss due to *P. downsi* larvae has been calculated at 20–55%—values that reduce growth rates or lead to mortality in other bird species (Gold and Dahlsten 1983). Observed effects on nestling growth (body mass, tarsus growth, feather growth) vary depending on species and year (Fessl et al. 2006b; Huber 2008; Knutie et al. 2016). As *P. downsi* larvae feed during the night, parental compensation through more feeding is often not sufficient, resulting in nestling death. Negative effects on nestling survival (16–100% nestling mortality) are high for all species that have been investigated except for the Galapagos mockingbirds (*Mimus parvulus*) (Knutie et al. 2016) (Table 9.2). The variability in observed mortality values for Darwin’s Finches can be explained by differences in parasitism pressure, varying environmental conditions in different study years, and the possibility of an “arms race” between *Philornis* and its hosts (see below).

9.4.1.1 Long-Term Consequences for Nestlings that Survive Parasitism

Beside enlarged and deformed nares (Fessl et al. 2006b; Galligan and Kleindorfer 2009; Kleindorfer and Sulloway 2016), *P. downsi* infestation may lead to crossed bills, observed in adult Green Warbler-finches (*Certhidea olivacea*) (B. Fessl, personal observation) and in a heavily infested Mangrove Finch (*Camarhynchus

Table 9.2 Findings of multiple-year studies on the effect of *P. downsi* on bird species in Galapagos (studies that do not provide data for individual species have been excluded) including parasite prevalence, parasite intensity in nests, associated nestling mortality

Species	Nest type	Average body size (g)	Average clutch size (range)	Habitat	Island	Years of data collection (rainfall)[a]	% parasite prevalence	Mean parasite intensity/ infested nests	Mean parasite intensity /chick	% nestling mortality from *Philornis*	Reference	Comments
Woodpecker Finch (WP)	Dome	20	2 (1–3)	Highland Scalesia forest	Santa Cruz	1998 (VH) 2000 (L) 2001 (M) 2002 (H) 2004 (L) 2005 (L)	100	67	30		Dudaniec et al. (2007)	Comparison between seven species (see other species below), higher parasite intensity in larger finches and for all species during 1998 El Niño, but no differences between habitat types
Small Tree-finch	Dome	13	2.4 (SC) 2.8 (Fl) (1–4)	Highland Scalesia forest	Santa Cruz	Same as WP	100	36	20		Dudaniec et al. (2007)	

(continued)

Table 9.2 (continued)

Species	Nest type	Average body size (g)	Average clutch size (range)	Habitat	Island	Years of data collection (rainfall)^a	% parasite prevalence	Mean parasite intensity/ infested nests	Mean parasite intensity /chick	% nestling mortality from *Philornis*	Reference	Comments
					Santa Cruz	2010 (H) 2012 (M)	100	38		56	Cimadom et al. (2014)	Lower nesting success in areas where *Rubus* sp. treated with herbicides; heavy rain events related to nest abandonment
					Santa Cruz	2014 (M) 2015 (M)	96 and 90				Cimadom et al. (2016)	*Philornis* in 22% of abandoned nests with eggs
					Floreana	2006 2008	100	30			O'Connor et al. (2010c) and shared *Philornis* database	Predation and *Philornis* influenced nest failure; positive relationship between rainfall (mm) and parasite load

					Floreana	2004–2013	100	29			Kleindorfer et al. (2014)	Parasite intensity increased across decade from 28 to 48, age at death changed from ~10 to 5 days old and mortality rate changed from 50 to 90% for all species combined; nests with many *Philornis* had early chick death
Large Tree-finch	Dome	18	2 (1–3)	Highland Scalesia forest	Santa Cruz	Same as WP	100	51			Dudaniec et al. (2007)	

(continued)

Table 9.2 (continued)

Species	Nest type	Average body size (g)	Average clutch size (range)	Habitat	Island	Years of data collection (rainfall)[a]	% parasite prevalence	Mean parasite intensity/ infested nests	Mean parasite intensity /chick	% nestling mortality from *Philornis*	Reference	Comments
Mangrove Finch	Dome	18	2 (1–4)	Lowland mangrove forest	Isabela	2007 2008		41		10–15	Fessl et al. (2010) and shared mangrove finch database unpublished	
						2013				37	Young et al. (2013)	
						2014 2015				33 and 65	Cunninghame et al. (2017)	
Medium Tree-finch	Dome	16	3 (2–5)	Highland Scalesia forest	Floreana	2006 2008	100	43 65	16 20	53	O'Connor et al. (2010c)	
						2004-2013	100	55			Kleindorfer et al. (2014) shared *Philornis* database unpublished	
Green Warbler-finch	Dome	8	2 (1–3)	Highland Scalesia forest	Santa Cruz	Same as WP	95				Dudaniec et al. (2007)	
						2010 (H) 2012 (M)	100	26		37	Cimadom et al. (2014)	
						2014 (M) 2015 (M)	98 and 94				Cimadom et al. (2016)	*Philornis* in 88% of abandoned nests with eggs

Vegetarian Finch	Dome	34	2.8 (2–4)	Arid zone	Santa Cruz	2013 (M) 2014 (M)	91	71	26	25	Heimpel et al. (2017)	
Small Ground-finch	Dome	14	3.2 (SC) 4.3 (Fl) (1–6)	Arid zone, highland Scalesia forest	Santa Cruz	Same as WP	99	40–low elevation 29–High elevation	21		Dudaniec et al. (2007)	
					Floreana	2004 2005 2006		8–low elevation 39–High elevation	3–Low elevation 16–High elevation		O'Connor et al. (2010b)	Higher parasite intensity led to lower fledgling success in the highlands but not in the lowlands

(continued)

Table 9.2 (continued)

Species	Nest type	Average body size (g)	Average clutch size (range)	Habitat	Island	Years of data collection (rainfall)^{a}	% parasite prevalence	Mean parasite intensity/ infested nests	Mean parasite intensity /chick	% nestling mortality from *Philornis*	Reference	Comments
Medium Ground-finch	Dome	17	(2–5)	Arid zone	Santa Cruz	Same as WP	100	39	19		Dudaniec et al. (2007)	
						2004 (L) 2005 (L) 2006 (L)	64–98			16–37	Huber (2008)	In wettest part of the season mortality was reduced; larvae fed on dead chicks; no effects of parasites on growth—high predation levels
						2008 (H)	96	39		96	Koop et al. (2011)	
						2009 (L)	83	36		86	Koop et al. (2013b)	
						2010 (H)	100	39		100	Koop et al. (2013a)	
						2012 (M) 2013 (M)	83 and 88	31 and 19		50 and 45	Koop et al. (2015)	
						2013 (M)	100	17		46	Knutie et al. (2014)	

Galapagos Mockingbird	Cup	51, 56 (females, males)	(1–5)	Arid zone	Santa Cruz	2012 (M) 2013 (M)		72 and 51		0	Knutie et al. (2016)	Increased nestling begging and parent provisioning in parasitized nests; higher hemoglobin levels and body mass values in fumigated nests

[a] Rainfall data was from the Charles Darwin Research Station meteorological weather station in Puerto Ayora, Santa Cruz Island (elevation: 2 m ASL) (CDF 2016) and was summed for the period July to June to take into account rainfall in the months preceding the bird breeding season. No meteorological data is available for Floreana and Isabela. It has to be noted that rainfall varies greatly within an island and thus the categories given might not reflect local rainfall at the study sites. VH > 1000 mm, H > 500 mm, M > 250 mm, L < 250 mm

Fig. 9.11 This Mangrove Finch was collected for captive breeding at 4 days old in 2015. It developed a cross-beak due to early *P. downsi* infestation in its nares. The bird fed by itself in the aviary but did not succeed in the wild. It died 3 days after its final release into natural habitat on Isabela Island (*see* Fig. 9.12). Photo: F Cunninghame

heliobates) individual that was hand-reared (F. Cunninghame, personal communication) (Fig. 9.11). The latter fed successfully in captivity, but subsequently could not find food under natural conditions. Studies on the ecological consequences of such malformations to surviving birds, e.g., reduced bill force, reduced survival, or altered singing abilities have not been carried out.

In well-established parasite-host relationships, adult birds can compensate for nestling blood loss by parasites through additional feeding (Tripet and Richner 1999). However, if food is limited or if the energy resources of adults are depleted, nestlings fledge with reduced weight and/or hemoglobin levels (Hurtrez-Boussès et al. 1997) as also observed in Galapagos for finch hosts of *P. downsi* (Dudaniec et al. 2006; Fessl et al. 2006b; Koop et al. 2011; Knutie et al. 2016). Weight at fledging is related to first-year survival in studied bird species (Magrath 1991) and low hemoglobin concentration lowers flight performance. This could affect predator avoidance and foraging behaviors (O'Brien et al. 2001) and might reduce survival probabilities and subsequent recruitment to the population. Fledglings of other species affected by other nest parasitic flies, such as *Protocalliphora*, have a reduced probability of survival (Streby et al. 2009). Thus, there may be even higher fitness costs related to *P. downsi* parasitism than found so far.

9.4.1.2 Susceptibility of Galapagos Bird Species to *P. downsi*

Several authors have found that parasite intensity varies in different species even when they share the same environmental conditions, suggesting that host traits (e.g., body mass, immune response, nest type, size and height, parental care, or an ability to compensate for blood loss) play a role in determining how many parasites are found in a nest (O'Connor et al. 2010b; Kleindorfer et al. 2014; Knutie et al. 2016). Other studies show that similar rates of parasitism in a nest affect host species differently under the same climatic conditions (Cimadom et al. 2014; Knutie et al. 2016, 2017). Some birds, such as mockingbirds, appear to be tolerant to *P. downsi* infestation and suffer little or no negative effects of parasitism, making them reservoir hosts and sources of flies (Knutie et al. 2016, 2017). What makes the Galapagos Mockingbird less vulnerable to parasitism by *P. downsi* is unclear, but it appears to be related to increased provisioning by parents and possibly to host size (Knutie et al. 2016). Vegetarian Finches (*Platyspiza crassirostris*) also show some levels of tolerance to *P. downsi* infestation and they are one of the largest Darwin's finches (Heimpel et al. 2017).

The degree of host susceptibility is also likely to be influenced by environmental conditions, such as the size of the nesting area and the spatial distribution of hosts (Kleindorfer and Dudaniec 2009), climate and/or food availability (Koop et al. 2013b; Cimadom et al. 2014). Bird species that are temporarily exposed to higher fly numbers due to climate (e.g., in times of drought flies congregate in highlands (O'Connor et al. 2010b), or species with restricted nesting areas may be particularly susceptible because clumped distributions of suitable hosts make it easier for *P. downsi* to find new hosts (Kleindorfer and Dudaniec 2009). For example, the Critically Endangered Mangrove Finch is restricted to a 30 ha mangrove forest that is surrounded by lava and sea (Fessl et al. 2010), essentially forming a small island (Fig. 9.12). There is some evidence that susceptibility to parasitism may increase when bird health is also affected by other factors such as

Fig. 9.12 One of the two remaining mangrove patches in north-western Isabela that harbors approximately 30 pairs of the Mangrove Finch. The mangroves are surrounded by bare lava; the arid zone vegetation lies approx. 600 m further inland. Flies are known to cross between the arid zone and mangrove forest. Photos: F Cunninghame

introduced predators, disease, food availability, and extreme climatic events (Fessl et al. 2010; Koop et al. 2013b; Cimadom et al. 2014). On the other hand, when food is plentiful hosts may be more tolerant. Recent studies on the threatened Mangrove Finch show higher fledgling survival rates toward the end of the breeding period when more food is available, although nests often contain the same number of larvae as earlier in the season (F. Cunninghame, personal communication). Additional research is needed to understand which species are more vulnerable and when.

9.4.1.3 Seasonal and Geographical Variation in Parasite Prevalence and Intensity

Typically, *Philornis* spp. show a continuous increase in prevalence and intensity per nest over the breeding season (Arendt 1985; Young 1993). Findings in the Galapagos Islands are not so clear-cut and suggest that there are geographical and climatic influences in interplay with parasite numbers (Table 9.2). In Galapagos, the bird-breeding season typically starts around mid-January at the beginning of the rainy season and lasts until April. Most bird species, however, are highly opportunistic breeders and attempt nesting as soon as conditions are favorable, i.e., when rain triggers some insect development as a food source for nestlings. Huber (2008) found higher number of parasites per nestling at the beginning of the season for the Medium Ground-finch (*Geospiza fortis*) at a lowland arid study site on Santa Cruz (Fig. 9.10); however, this seems to be related to smaller clutch sizes at the onset of the breeding season rather than to higher parasite density at this time of the year. We are not aware of another study in Galapagos that has found differences in parasite intensity over the season.

Parasite prevalence (percentage of infested nests) did not appear to differ over the breeding season at study sites on Santa Cruz, Floreana, or Isabela (Fessl and Tebbich 2002; Dudaniec et al. 2007; Huber 2008; Kleindorfer et al. 2014; Cunninghame et al. 2017) (Table 9.2). The absence of a clear trend in parasite prevalence in these studies, however, might be an artifact of low to absent bird nest monitoring carried out outside the main bird breeding season (January to April), in particular during the very early stages of the nesting season.

One of the few species with data from both highland and lowland zones (Fig. 9.10), the Small Ground-finch, showed an extremely low parasite load (eight larvae per nest) in the lowlands of Floreana compared to the highlands (around 40 parasites per nest) (O'Connor et al. 2010b), a pattern not found in Santa Cruz (Dudaniec et al. 2007) (Table 9.2). In these multiple-year comparisons, all study years were very dry in Floreana (2004–2006) whereas two out of the six study years on Santa Cruz had abundant rainfall (1998, 2002). Additional studies are required to determine whether there are elevational differences in parasite prevalence.

9.4.2 Host-Parasite Arms Race: Advances by the Parasite

Changes in *P. downsi* behavior have been recorded since it was first found in bird nests in Galapagos in 1997; in turn, this has affected bird reproductive success. We discuss here two behaviors that appear to be adaptations of *P. downsi* to the abnormally high levels of intraspecific competition that this parasite is facing in the Galapagos Islands: early egg laying in nests and increased parasite densities in nests.

9.4.2.1 Early Egg Laying

Philornis downsi larvae are now found in nests during the incubating phase, showing that they feed on blood of the incubating female birds. This behavior was first observed in 2012 in nests of Small Tree-finches (*Camarhynchus parvulus*) and Green Warbler-finches at Los Gemelos, Santa Cruz (Cimadom et al. 2016). In earlier studies, nests that failed during incubation had no larvae (Fessl and Tebbich 2002). Since the first reports in 2012, it has also been observed in a study of *P. downsi* infestation of Vegetarian Finch nests in the lowlands of Santa Cruz (G. E. Heimpel unpublished). Another line of reasoning supporting the hypothesis of adult feeding by *P. downsi* larvae comes from immunological data. On Santa Cruz, Huber et al. (2010) and Koop et al. (2013a) found that adult female Medium Ground-finches from *P. downsi*-infested nests produced antibodies against *P. downsi* proteins while females from *P. downsi*-free nests did not. These females also had higher levels of antibodies than males did in both studies. Since only female birds incubate eggs and brood young nestlings these results suggest strongly that adult birds had been parasitized by *P. downsi*. In Floreana, Kleindorfer et al. (2014) reported larger numbers of first-instar larvae in nests with young chicks (<5 days old) in 2010–2013 compared to 2004–2008, suggesting earlier egg laying behavior of the flies, though not as early as on Santa Cruz.

The potential implications of *P. downsi* larvae feeding on adult female hosts include nest abandonment if females are bothered by the feeding larvae or energy costs resulting in the need to feed more. In addition, incubation time might be reduced, leading to irregular temperatures in the nest and possibly longer development times of chick embryos. Alternatively, reduced incubation times in areas with higher ambient temperature and strong sun may lead to overheating of nests and embryo or chick death. In an experimental study on Blue Tit nests (*Cyanistes caeruleus*) infested with flea lice, hatching success was reduced by parasitism and females abandoned infested nests more readily between egg laying and the first days after hatching (Oppliger et al. 1994). Food availability and the energetic state of the female can play an important role as shown by supplementary feeding of incubating females in parasite-infested nests resulting in increased hatching success (Nilsson and Smith 1988). A comparison of parental behavior in the early chick phase in parasitized and unparasitized nests showed significantly reduced brooding times for both Mockingbirds and Medium Ground-finches in parasitized nests, but no difference in the overall time spent at the nest, indicating that adult birds try to avoid the parasites (Koop et al. 2013b; Knutie et al. 2016).

Early infestation of nests means that recently hatched nestlings are confronted with second-or third-instar larvae rather than first-instar larvae, thus suffering greater blood loss that might quickly lead to death (Gold and Dahlsten 1983; Fessl et al. 2006b). Indeed, age of chick death has changed: whereas in the first studies chick death was observed primarily in the late feeding phase (>7d old), this has now changed to the early feeding phase on both Floreana and Santa Cruz (Fessl and Tebbich 2002; Cimadom et al. 2014; Kleindorfer et al. 2014).

9.4.2.2 Increase in Parasite Intensity

Kleindorfer et al. (2014) suggested that parasite intensity has increased over the last 10 years in the nests of three bird species on Floreana: the Small Ground-finch, the Small Tree-finch, and the Medium Tree-finch (*Camarhynchus pauper*). This trend has not been observed in Tree Finches on Santa Cruz (Table 9.2), where parasite intensity/nest has not changed substantially between 1998 and 2012 for two species with comparable data sets from the humid Los Gemelos area—the Green Warbler-finch and the Small Tree-finch (Fessl and Tebbich 2002; Kleindorfer and Dudaniec 2009; Cimadom et al. 2014). Similarly, in the arid zone of Santa Cruz, *P. downsi* intensity in Medium Ground-finch nests showed no noticeable trend between 2008 and 2013 (Koop et al. 2015)—though data from earlier years are missing. These apparent differences in trajectories of parasite intensity between Floreana and Santa Cruz are not well understood. Floreana is a smaller and overall drier island than Santa Cruz, so the smaller bird population overall and the shorter breeding window compared to Santa Cruz may induce *P. downsi* crowding under a broader set of circumstances.

9.4.3 Host-Parasite Arms Race: Advances by the Host

As we have just noted, data suggest that flies have changed their life cycle since they colonized the Galapagos Islands to deal with a novel environment and hosts. But what of the hosts? Are birds able to develop strategies similar to those found in other parts of the world to deal with novel parasites? We discuss a number of behaviors of birds elsewhere in the world that are known adaptations to ectoparasites and their importance for *P. downsi* invasion in Galapagos.

9.4.3.1 Avoidance of Infested Nests

This is a known behavior of bird species associated with parasites that enter a diapause state to overwinter in the nest (Oppliger et al. 1994), but is not a behavior that is typical of most birds in Galapagos because most bird species there do not normally re-use nests even if they attempt nesting soon after nest failure. The Galapagos Flycatcher and the Galapagos Dove sometimes use old finch or mockingbird nests that could still harbor larvae or pupae (Grant and Grant 1979). And some Galapagos landbird species are known to incorporate old nest material or feathers into new nests which could increase the risk of bringing *P. downsi* larvae into a newly built nest (*see* Lincango et al. 2015; A. Cimadom, personal communication and C. Pike, personal communication). Darwin's Finch nests, however, are often built relatively close to current or recent conspecific nests and Kleindorfer et al. (2009) found that different species of Darwin's Finches tend to nest close to each other probably to benefit from lower predation rates. This behavior likely results in a higher parasite load for these nests.

9.4.3.2 Incorporation of Repellent Material into Nests

Elsewhere, bird species are known to take aromatic plant material to nests (Clark and Mason 1988; Gwinner et al. 2000), which reduces biting insects and/or bacterial growth. In Darwin's Finches, an interesting behavior was observed for the first time in 2012: various species of finches (Green Warbler-finch, Small Tree-finch, Small Ground-finch, Medium Ground-finch) were seen rubbing themselves with leaves of the endemic tree Guayabillo (*Psidium galapageium*). Experiments have shown that this plant has a repellent function for mosquitoes as well as for *P. downsi* larvae (Cimadom et al. 2016). Whether this behavior has evolved in response to flies infesting nests earlier as mentioned above and the need of incubating females to protect themselves need to be investigated further.

9.4.3.3 Mothers That Have Been in Contact with Parasites Can Pass Antibodies to Offspring

Positive, parasite-induced maternal effects in the form of immunoglobulins transferred via the egg have been shown to affect nestling survival in the Great Tit (*Parus major*)/hen flea host-parasite system in some studies (Heeb et al. 1998; Buechler et al. 2002) while other studies found that egg mass (Tschirren et al. 2009) or nestling size (Gallizzi and Richner 2008) were better predictors for nestling survival. As noted above, female Medium Ground-finches developed antibodies for *P. downsi* (Huber et al. 2010; Koop et al. 2013a), and females with higher levels of *P. downsi*-specific antibodies tended to have fewer parasites in the nest. However, the antibody response by females did not lead to higher fledgling success (Koop et al. 2013a). Neither adult males nor nestlings themselves showed any evidence of *P. downsi*-specific antibodies (Koop et al. 2011, 2013a; Knutie et al. 2016). Studies on transgenerational immunity are needed to better interpret these findings.

9.4.3.4 Parents Reduce Parasite Load by Nest Cleaning and Allopreening

This behavior is observed in many bird species (Christe et al. 1996a; Hurtrez-Boussès et al. 1998; Simon et al. 2004) and has also been observed in Galapagos (O'Connor et al. 2010a). However, cleaning did not significantly increase nestling health or nesting success when parasitized and unparasitized nests were experimentally compared (Koop et al. 2011; Koop et al. 2013b; Knutie et al. 2016). Parents on occasion eliminate dead or very weak chicks from the nest (O'Connor et al. 2010a; Lincango et al. 2015), a form of nest sanitation, but nothing is known about the impact of this behavior on parasite incidence.

9.4.3.5 Compensation by Increasing Nestling Provisioning Rates

Studies on *Protocalliphora* species have shown that parents can compensate nestlings for energy loss from parasites when food abundance is high, reducing differences in growth or mortality rates compared to uninfested nestlings (Hurtrez-Boussès et al. 1998; Merino and Potti 1998). Parents that increased the provisioning rates to counteract parasitism, however, paid a fitness cost with reduced chances of year-to-year survival (Wesolowski 2001), reduced future reproduction (Richner and Tripet 1999), or reduced immune function leading to increased receptivity to other diseases (Richner et al. 1995; Oppliger et al. 1996). For the arid zone of Santa Cruz Island, higher provisioning rates within parasitized nests compared to parasite-free nests were observed in Mockingbirds but not in finches (Knutie et al. 2016). Moreover, higher provisioning rates by Mockingbirds were triggered by higher begging rates, a behavior not observed in finches (Knutie et al. 2016). On the contrary, O'Connor et al. (2013) observed that the weakest nestling, i.e., the nestling that was parasitized most during the night, begged less and as a result received less food; it probably was too weak to engage in begging behavior (Christe et al. 1996b). Nothing is known about the long-term impact of extra nestling provisioning on the health or fitness of parents of *P. downsi*-infested nestlings in Galapagos.

9.4.3.6 Nestlings Use Tactics Against Parasites

The nestlings of various bird species can themselves act against parasites by removing them or by moving in relation to nest mates to reduce contact with parasites (Simon et al. 2005). In the case of *P. downsi* in Galapagos, preening represented less than 1% of the activity of finch nestlings in infested nests in one study (Koop et al. 2013b). However, videos have shown that only one nestling receives the most intensive larval feeding at a given time probably as a result of stronger nestlings standing on top of weaker or already dead ones and thus avoiding contact with the parasites at the bottom of the nest (O'Connor et al. 2010a). Additionally, there are some observations of premature fledging in nests with single nestlings after the siblings died (F. Cunninghame, personal communication).

9.5 Implications for the Conservation of Galapagos Ecosystems

Philornis downsi is classified as one of the most invasive insects in the Galapagos Islands (Causton et al. 2006) and is deemed one of the most important threats to landbird conservation in the archipelago. It is suspected that it is the key factor responsible for the decline of landbirds on Santa Cruz (Dvorak et al. 2012) and Floreana (Grant et al. 2005; O'Connor et al. 2010c; Dvorak et al. 2017) and is the main reason for a current head-starting project to prevent the extinction of the Mangrove Finch (Cunninghame et al. 2015)—*see* Sect. 9.6. Currently, 14 of the 28 endemic small terrestrial bird species are on the list of threatened species (IUCN 2016).

9.5.1 Vulnerability of Finches Versus Mockingbirds

Several studies suggest that bird species with small clutches may be at a higher risk from parasitism because the number of *P. downsi* larvae in a nest can be high even when brood size is small. Thus, the negative effect of *P. downsi* will be higher for species with an average clutch size of two such as the Tree Finches (*Camarhynchus* spp., *Certhidea* spp.) than for species with average clutch sizes of three and more such as the Ground Finches (*Geospiza* spp.) (Table 9.2). Four species of the former group have been assigned a threat status under IUCN. The island endemics Medium Tree-finch and Mangrove Finch are listed as Critically Endangered and two more broadly distributed species, Woodpecker Finch and Large Tree-finch (*Camarhynchus psittacula*), were up-listed only recently to Vulnerable (IUCN 2016) based upon observed declines on inhabited islands (Dvorak et al. 2012). Field studies and population viability analyses suggest that *P. downsi* has played a major role in the negative population dynamics of the two Critically Endangered species (Fessl et al. 2010; O'Connor et al. 2010c; Young et al. 2013; Rodríguez and Fessl 2016); the consequences of *P. downsi* parasitism on the other two species is largely unstudied. Furthermore, a population viability analysis showed that populations of the widely distributed Medium Ground-finch could become extinct in the next 100 years, especially if environmental stressors increase (Koop et al. 2015).

On the other hand, the studies by Knutie et al. (2016) on the abundant Galapagos Mockingbird on Santa Cruz show that this species is more resilient to parasitism by *P. downsi* than are the finches. This provides some hope for the endangered Floreana mockingbird (*Mimus trifasciatus*), which is restricted to two satellite islands off Floreana and is a host of *P. downsi* as well (Wiedenfeld et al. 2007; Hoeck et al. 2010). Preliminary findings suggest that nesting success by *M. trifasciatus* is not significantly affected by *P. downsi* parasitism (L. Ortiz-Catedral, in prep.).

9.5.2 Potential Ecosystem Effects of Finch Declines

Low reproductive success of Darwin's Finches and other landbirds may also have an effect on community dynamics, ecosystem structure, or the composition of natural ecosystems. This is in part due to finches being involved in mutualistic interactions with other species. Most landbird species in Galapagos feed on flowers and/or carry pollen (Traveset et al. 2015) and some species are seed dispersers of endemic plants (Guerrero and Tye 2009; Heleno et al. 2013). Reduction of passerine abundance, in particular of species that are considered important pollinators or seed dispersers (Heleno et al. 2011; Heleno et al. 2013; Nogales et al. 2017), could potentially affect vegetation and ecosystem structure (Heleno et al. 2011, 2013) in ways that we do not yet understand. Three species of Ground Finches (*Geospiza* spp.) are known to remove parasitic ticks from the bodies of marine iguanas and giant tortoises (Carpenter 1966; MacFarland and Reeder 1974) but the importance of this activity to iguana or tortoise health has not been determined as far as we are aware. More research is needed to investigate mutualisms and the indirect impacts that *P. downsi* may be having on Galapagos ecosystems by leading to declines in landbird populations.

9.6 Conservation Actions

Since 2012, considerable effort has been placed on understanding the biology and ecology of *P. downsi* and developing methods to reduce its impacts on endemic birds in Galapagos. Our main focus is on developing methods for protecting threatened birds in the near-term (hand-rearing nestlings, trapping adult flies using attractants, and use of insecticides in nests) while longer-term solutions such as biological control, mating disruption, and the Sterile Insect Technique can be found for permanently reducing fly populations. Particular care must be employed to use techniques that minimize environmental damage because of the fragile nature of the ecosystems in the Galapagos Islands.

9.6.1 Short-Term Solutions

We discuss three classes of short-term solutions aimed at reducing the negative effects of *P. downsi* in Galapagos: temporary captive-breeding of bird nestlings for species that are highly threatened and subject to high levels of fly attack, using insecticides against larvae in nests, and trapping adult flies.

9.6.1.1 Captive Breeding

Once it was determined that nests of the Critically Endangered Mangrove Finch were associated with high rates of parasitism by *P. downsi* (Fessl et al. 2010), immediate measures were needed to protect nestlings from parasites. The Mangrove Finch is one of the rarest birds in the world with approximately 30 breeding pairs left in the wild in a small (30 ha) patch of mangroves on the coast of western Isabela Island (Fessl et al. 2010; Young et al. 2013; Fig. 9.12). Intervention was particularly important at the onset of the breeding season when nestlings seem to be particularly vulnerable to parasitism (Cunninghame et al. 2015). For the first time in Galapagos, a captive breeding program for birds was implemented to give nestlings a "head-start" on *P. downsi* before being released into the wild. For this program, eggs were transported to a biosecure rearing room on Santa Cruz Island where nestlings were carefully reared until they were approximately 6 weeks old after which they were returned to the mangrove habitat on Isabela (Cunninghame et al. 2015). Steps to ensure that finches learned to feed independently and communicate with conspecifics were also put in place. On being returned to the wild, the finches were held in aviaries for an additional 4–6 weeks before release. This program has been running for the last four breeding seasons (2014–2017) and over this time 41 finches have been reared successfully and are now back in their natural habitat; some have even started to establish territories (see Cunninghame et al. 2015, 2017). The aim of this project is not to develop a permanent captive breeding population, but instead to circumvent *P. downsi* infestation until an adequate control method is in place.

9.6.1.2 Insecticides

In the short term, the safe use of low levels of bird-friendly insecticides may be the only viable method for protecting nests and several insecticides are being evaluated. Experimental studies to exclude parasites from nests with synthetic pyrethroids including permethrin (Knutie et al. 2013, 2014, 2016; Koop et al. 2013a; Kleindorfer and Sulloway 2016) and pyrethrin (Fessl et al. 2006b; O'Connor et al. 2013) have shown that insecticide application can significantly reduce *P. downsi* larval numbers and is probably the best option to pursue. A literature-based risk assessment revealed no short-term effects of permethrin on adult or hatchling bird survival (Causton and Lincango 2014). However, a recent experimental study suggests that nestling health may be affected by permethrin under some application and dose scenarios (Lopez-Arrabé et al. 2014), and little is known about effects on long-term reproductive success or bird health (Causton and Lincango 2014). This highlights the importance of continuing the evaluation of the risks of using this insecticide in the nests of birds with very low population numbers such as the Mangrove Finch. Research is currently being conducted to evaluate long-term impacts of using this insecticide. In the event that it is safe for the long-term fitness of finches, permethrin could be used to protect birds in the field.

Fig. 9.13 (A) Small Ground-finch carrying impregnated cotton to its nest; (B) injection of permethrin to a nest of the Small Tree-finch at Los Gemelos, Santa Cruz. Photos: S Knutie, C Leuba

Knutie et al. (2014) have recently developed an innovative method to deliver permethrin (or other insecticides) to Darwin's Finch nests in the field (Fig. 9.13): they deployed cotton impregnated with a permethrin solution and showed that four species of finches used this cotton in nest construction and that this led to significantly lower *P. downsi* infestation. A major advantage of this method is the directed placement of insecticide within nests which would both minimize impact on non-target arthropods and also facilitate treatment of otherwise hard-to-access nests. A potential risk of the methods is that nestlings are directly exposed to the insecticide dermally and the adult birds carrying the impregnated cotton are directly exposed through the inside of the beak as well. While this system seems to have worked with some finch species that readily use cotton in nest construction (Medium and Small Ground-finches, Common Cactus-finches (*Geospiza scandens*) and Vegetarian Finches (Knutie et al. 2014)), it appears that not all birds will take cotton back to nests, including the Mangrove Finch (F. Cunninghame, personal communication). Trials are being conducted to determine whether other material used for building nests is feasible for insecticide incorporation (e.g., Mangrove Finches use algae). Other methods are being tested to deliver the insecticides to the nests minimizing contact with chicks, including using poles with syringes to inject permethrin into the sides of the nest (Cimadom et al. unpublished) (Fig. 9.13).

9.6.1.3 Trapping Adult *P. downsi*

Intensive efforts are being made to understand the chemical ecology of *P. downsi* with the aim of finding olfactory cues that can be used to trap flies for population monitoring and suppression. Potential cues could include food odors, nest or bird

Fig. 9.14 Yellow traps with yeast lures are placed at different heights at the Mangrove Finch nesting area to test effectiveness in capturing flies. Photo F Cunninghame

odors or pheromones produced by the flies themselves. Fermenting fruits are a preferred food of adult *P. downsi* and trials have been conducted on a variety of fruits including papaya and blackberry. However, it appears that a yeast-sugar solution is just as effective. Studies were carried out to identify the principal compounds in this mixture that are attractive to *P. downsi* as a means for developing a lure (Cha et al. 2016) and studies are now underway to develop longer lasting lures (A. Mieles and S. Teale, unpublished). Fly pheromones may be another option for attracting flies to traps and could also have potential to be used at a larger scale to disrupt mating (*see* below). Laboratory analyses of cuticular and genital extracts suggest that the composition of lipids of *P. downsi* differs between sexes and experiments in the field suggest that the male is the attractive sex (Collignon et al. 2014, Mieles et al. in prep). This is promising as it suggests the possibility of developing a female-specific lure. Additional trials are required to determine whether pheromones can be used as a lure, perhaps in combination with food odors.

Mass-trapping is an option for suppressing *P. downsi* populations in the nesting areas of threatened birds, but the method has to be effective enough to reduce parasitism rates and, if possible, trap flies before they lay eggs. Traps used with lures to date, for example, have not been effective in catching flies in the habitat of the Critically Endangered Mangrove Finches (Fig. 9.14). These finches, restricted to a small area of mangrove swamp, nest high in the canopy (up to 23 m) and it may be that traps would need to be hung extremely high to capture *P. downsi* at this site.

9.6.2 Long-Term Solutions

In this section, we discuss three potential long-term management solutions for *P. downsi* in the Galapagos Islands—the release of one or more specialized biological control agents, the release of sterile male *P. downsi*, and mating disruption.

9.6.2.1 Importation Biological Control

Importation biological control (also known as classical biological control) using natural enemies from the fly's native geographic range is currently the most promising option for permanently controlling fly populations. While importation biological control can entail significant risks and has sometimes been used irresponsibly in the past, protocols for risk assessment and mitigation have greatly increased the safety of this tactic over the past few decades (Heimpel and Mills 2017). Biological control has been used successfully and safely to control invasive species in natural ecosystems and is in some cases the only management option available in these settings (Van Driesche et al. 2010). Furthermore, although initial costs can be high to cover exploration and intensive safety testing studies, costs are low once the agent is established and the benefits are self-sustaining since they are conferred by living organisms.

To date, a single biological control project has been implemented in Galapagos: control of the Cottony Cushion Scale (*Icerya purchasi*), a herbivorous insect that is native to Australia, by the specialized predatory ladybug (*Rodolia cardinalis*) (Causton 2009). This release followed extensive ecological safety testing (Causton et al. 2004; Lincango et al. 2011) and it led to *R. cardinalis* establishing and spreading well once it was released beginning in 2002 (Calderon Alvarez et al. 2012; Hoddle et al. 2013). Post-establishment studies showed greatly reduced levels of Cottony Cushion Scale coupled with the recovery of endemic plant populations while safety to non-target species was evaluated and confirmed in field studies (Hoddle et al. 2013). This project therefore shows that importation biological control can be used successfully and safely in Galapagos to protect biodiversity.

For *P. downsi*, the most likely biological control agents would be parasitoids, as many species are highly specialized. Parasitoids are lethal parasites; females lay eggs in (or on) host insects and the resulting larvae consume the host individual, killing it in the process (Godfray 1994). Hundreds of parasitoid species have been used as biological control agents all over the world throughout the 19th and 20th centuries, primarily in agricultural and forest settings (Cock et al. 2016; Heimpel and Mills 2017). Since the discovery of *P. downsi* and other *Philornis* species on mainland Ecuador, studies are being carried out to document the parasitoid complex there. To date, five species of parasitoid wasps have been found attacking four species of *Philornis* that themselves collectively attack 11 species of birds at two sites in Western Ecuador (Fig. 9.15). Together these parasitoids attack and kill an estimated 8–20% of *Philornis* pupae within bird nests, depend-

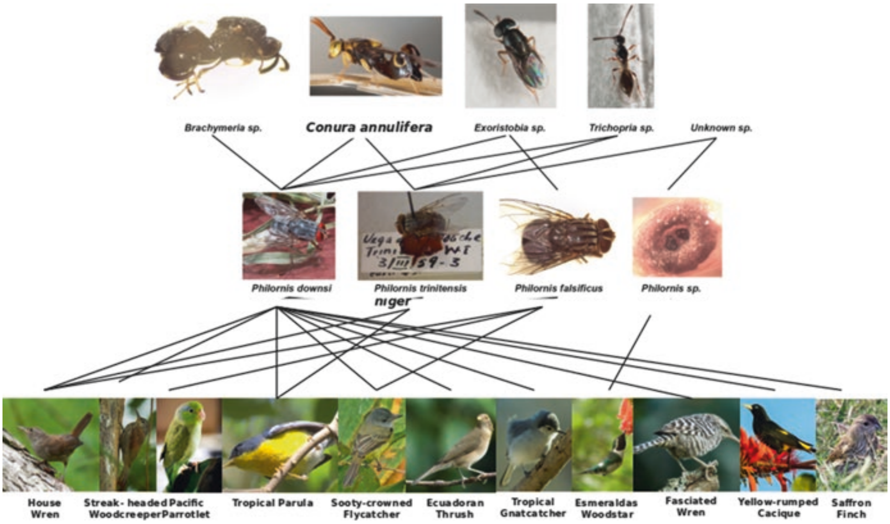

Fig. 9.15 Associations between bird species, *Philornis* species, and parasitoid species at two sites in western mainland Ecuador (*see* Fig. 9.6) over 3 years of observation (2013–2015) using various sampling methods. Lines indicate associations. Data compiled from Bulgarella et al. (2015) and additional sampling by GE Heimpel, M Quiroga and M Bulgarella. Photos: *Brachymeria* sp.—JS Dregni; all other parasitoids and P. *downsi*—D Hansen (U of MN); *Philornis* sp.—GE Heimpel; *P. falsificus* and *Philornis niger*—M Bulgarella. Birds: House Wren—CheepShot CC BY 2.0; Streak-headed Woodcreeper, Yellow-rumped Cacique, Tropical Gnatcatcher, Fasciated Wren—F Veronesi from Italy Costa Rica, Pantanal-Brazil and South Ecuador CC BY-SA 2.0; Pacific Parrotlet—SC Griffin CC BY-SA 3.0; Tropical Parula—D Sanches from Brasil CC BY-SA 2.0; Sooty-crowned Flycatcher, Ecuadorian Trush, Saffron Finch—L Kee from Singapore CC BY-SA 2.0; Esmeraldas Woodstar—Bertdichrozona at English Wikipedia CC BY-SA 3.0

ing upon the site and the year (Bulgarella et al. 2015, 2017). Of the parasitoid species, one is known from the literature—*Conura annulifera* (Chalcididae). This species has been reported only from *Philornis* spp. (Burks 1960; Delvare 1992; Couri et al. 2006) and is therefore a promising candidate for importation biological control. Indeed, laboratory studies corroborate these observations and indicate specificity to *Philornis* as well (Bulgarella et al. 2017). Since no native or endemic *Philornis* species occur in Galapagos (Sinclair 2015), a release of *C. annulifera* would pose little risk to endemic species if the conclusion of *Philornis* specificity is held up in further studies.

For the evaluation of biological control agents, as well as for evaluating the feasibility of other control techniques, being able to rear *P. downsi* is an important prerequisite. In spite of its adaptability to different climates and its proclivity for laying eggs in captivity even in the absence of hosts, *P. downsi* has proved difficult to rear in laboratory in spite of intensive efforts. The main stumbling block has been getting flies to mate consistently in the laboratory. Rearing the larvae has been another limiting factor, although advances have been made in developing artificial diets (Lahuatte et al. 2016) and using domestic birds, particularly the Society Finch (*Lonchuria striata domestica*), as a surrogate host (Bulgarella et al. 2017). To our knowledge, both of these rearing methods for *P. downsi* represent the first time that any avian parasitic fly species has been reared in the laboratory.

9.6.2.2 Sterile Male Release

Successful rearing is also a prerequisite for evaluating the potential for using the Sterile Insect Technique (SIT) for controlling *P. downsi*. SIT is highly species-specific and environmentally benign and several pest insects have been successfully controlled and even eradicated from some islands and countries using this technique. For example, Screwworm Flies (*Cochliomyia hominivorax,* Calliphoridae) were successfully eradicated from the southwestern United States and northern Mexico using this method in the 1960s (Klassen and Curtis 2005). This technique works by releasing millions of males that have been made sterile by radiation. Recent research developments suggest that insects can also be genetically manipulated to achieve sterilization (Alphey 2014). In these cases, females that mate with sterile males are not able to reproduce and over several generations the population is diminished and in some cases driven to extinction (Vreysen et al. 2007). The feasibility of using this control option in Galapagos cannot be determined until we have a better understanding of the biology and ecology of the fly and it can be reared in sufficiently large numbers. Biological variables that increase the success of SIT programs include high productivity in the laboratory (high fertility, high fecundity, short life cycle, and longevity) and sufficient post-release fitness to compete with wild flies (survival capacity, temperature tolerance, and fertility) (Sorensen et al. 2012).

9.6.2.3 Mating Disruption Using Pheromones

Large-scale applications of insect sex pheromones can interfere sufficiently with mate attraction (called “mating disruption”) to significantly reduce damage caused by some pests (El-Sayed et al. 2006; Suckling 2014). This approach has been used to control agricultural pests such as the Codling Moth (*Cydia pomonella* L.) (Witzgall et al. 2008) and has also been used in natural ecosystems to eradicate, control, or contain invasive species, e.g., against insects such as Gypsy Moth (*Lymantria dispar dispar* L.) (Sharov et al. 2002; Brockerhoff et al. 2012). Mating disruption has been particularly successful against Lepidoptera and it remains to be seen whether it could be an option for *P. downsi*. Although it has been determined that some chemicals produced by *P. downsi* males elicit responses in females (Collignon et al. 2014, Mieles et al. in prep) additional research is needed to determine whether this technique is an option for long-term control.

9.7 Conclusions

Philornis downsi attacks almost all of the small landbird species native to the Galapagos Islands. According to the IUCN (2016), 14 of 28 small landbird species endemic to the Galapagos are threatened; however, recent surveys on inhabited islands suggest that at least six other species have rapidly declining populations (Fessl et al. 2017). Management of *P. downsi* is crucial to prevent further declines of landbirds and restore communities. The Galapagos Landbird Conservation program managed by Charles Darwin Foundation and Galapagos National Park Directorate, with international collaborators, is collecting information on population status and health of small landbirds throughout the archipelago in order to understand what species and habitats are priorities for management intervention. Now that *P. downsi* and other *Philornis* species have been reported from mainland Ecuador (Bulgarella et al. 2015), it is also essential that additional introductions to the Galapagos Islands are prevented. A strong border and persistent monitoring will be essential to protect the iconic bird fauna of the Galapagos from further invasions.

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Part V
Challenges for Management

Chapter 10
Domestic and Peridomestic Animals in Galapagos: Health Policies and Practices

Luis R. Padilla, Nicole Gottdenker, Sharon L. Deem, and Marilyn Cruz

Abstract The wildlife of the Galapagos Islands faces the threat of disease due to spillover from introduced domestic and peridomestic species. Many domestic species benefit the roughly 25,000 residents and 250,000 visitors that travel to the islands every year. Although expanded human activities and the necessary agricultural and trade practices to support them are a potential concern for long-term sustainability of endemic species, the thriving economy behind this prime ecotourism destination is a possible asset and solution to protect it. Local agencies and strong, comprehensive management policies that are adaptable to rapidly changing conditions must be in place to guard against known and unknown disease threats.

Keywords Introduced species • Disease threat • Pathogen spillover • Conservation agencies

10.1 Introduction

Europeans arrived in the Galapagos Islands in the 1500s, and the islands have been permanently inhabited by humans since the 1800s. In the last two centuries of human settlement, many animal species have been introduced for agricultural use, human

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companionship, and others have been inadvertently introduced as the result of human activities. Habitat modification and degradation by humans or introduced animals, globalization of commerce, trade, transport, and the ease of international travel have been driving factors for recent introductions. Continued introduction of species exotic to the Galapagos Islands is a significant threat whose impact is difficult to predict. Rapid population growth, tourism, and the need to support human activities in the Galapagos Islands present challenges that, while not unique to this archipelago, require mitigation practices to protect and support its unique endemic biodiversity.

The effects of introduced species on endemic species are well documented elsewhere and include direct and indirect competition, predation, morbidity, and mortality caused by introduced pathogens. Infectious disease spillover from introduced to native species is a significant and potentially catastrophic threat to island endemic species, as they may have evolved in the absence of many pathogen pressures. In order to maintain healthy, robust, and self-sustaining populations of endemic species, comprehensive management policies must be in place to prevent disease introductions and cannot be limited by only mitigating the known species or the pathogens that they are known to carry: they must be based on best practices to exclude possible as well as known risks.

The Galapagos Islands is an area of rapid, recent population growth. A 2015 census by the Ecuadorian National Institute of Statistics and Censusing (ecuadorencifras.gob.ec) showed that the population had grown roughly by 9.5% in the previous 5-year period to 25,244 residents. The tourism industry is booming, with 223,587 visitors in 2015 (Boletin Galapagos 2015), and averaging 13 days per visit. Tourism revenue in the Galapagos Islands in 2015 was an estimated 268 million US dollars. Supporting this thriving tourism industry and growing local population creates a high demand for agricultural production, imports, and other services to sustain them. The people of Galapagos (residents and visitors) are as much a part of the current Galapagos Islands and its heritage as the endemic wild species that make it a prime global ecotourism destination. The conservation and preservation of the Galapagos Islands hinges directly on the success of efforts to manage the interplay between humans, domestic animals, wildlife, and ecosystems.

An understanding of the existing policies and the agencies that establish them, as well as what threats they mitigate, is important to continually revise and strengthen the necessary long-term sustainable management practices. Because threats are likely to change over time, agencies and policies must be accordingly adaptable. Without these policies, unmitigated anthropogenic forces threaten to become the major evolutionary force in the Galapagos Islands (Deem et al. 2010a). Chapter 2 (Colonization of Galapagos birds—identifying the closest relative and estimating colonization) summarizes the 12 bird species that were introduced by humans and how they made it to the Galapagos Islands, and acknowledges the threat of pathogen introduction and transmission to native birds. In this chapter, we first summarize disease threats that introduced species pose to native species. These threats can be grouped into some general categories:

1. By causing habitat degradation and/or loss, or through ecological interactions such as competition or predation, introduced species can impact the population size and distribution of native species, increasing the severity of a disease epidemic on reduced populations (or more densely distributed populations).
2. By modifying habitat, introduced species can increase the habitat's suitability for maintaining a pathogen.
3. By serving as primary sources or vectors of infectious disease, introduced species can transmit pathogens to naive and susceptible endemic species.
4. By serving as maintenance hosts for diseases with epizootic potential, introduced species can increase the possibility of outbreaks in the endemic populations.
5. By introducing their own host-adapted strains of common pathogens, introduced species may alter the prevalence of existing, circulating pathogen strains, possibly diluting the endemic strains that may have co-evolved with endemic host species. An endemic species may then be exposed to a different strain, increasing the likelihood of disease epizootics.
6. By changing the social structure, behavior, and population dynamics of native species, introduced species can lead to altered disease transmission processes in native species.
7. By being managed in some way that changes resource availability (food, water, shelter, nest sites), introduced species can lead to altered native species habitat use, exposure to high-risk environmental factors, predation, or altered social dynamics that change the rate of pathogen transmission.

Mitigating threats to native species is far more complex than a theoretical elimination of a pathogen or an introduced species. Eradication of some introduced, invasive species and restoration of the former habitat is the ideal scenario in many instances, but is not feasible for all species and may not necessarily be advantageous in the context of a balanced, sustainable management strategy. Healthy domestic agricultural species can have a significant role in sustaining local economies and indirectly maintaining healthier ecosystems. Policies should be aimed at managing the domestic and peridomestic animal populations (through regulation, population control, maintenance of healthy animals, and eradication where applicable), mitigating the risk of disease transmission and, mitigating the threat of inadvertent introductions, and protecting habitats from damage by animals. In addition, despite the focus on individual species and specific diseases being introduced by them, a growing realization is that the disruption of the processes that maintain balanced, healthy ecosystem is likely to have much more profound and persistent effects on the overall maintenance of biodiversity in areas of high endemism.

This chapter has three main parts: the regulatory agencies and their jurisdiction within the Galapagos Islands, the known and possible pathogen threats to specific native taxonomic groups, and the possible action items that have been identified to continue to mitigate these risks.

10.2 Agencies and Their Responsibilities

The people of the Galapagos Islands and the Ecuadorian government have long recognized the importance of biosecurity in preserving the uniqueness of this ecological resource. Roughly 97% of the islands remain uninhabited by humans, and efforts to maintain pristine wild ecosystems are aimed at the long-term sustainability of this top ecotourism destination and national source of pride. Current regulations for maintaining biosecurity in the Galapagos Islands are under the jurisdiction of the Agency for Regulation and Control of Biosecurity and Quarantine for Galapagos, also known as "ABG" for its Spanish acronym (*A*gencia de Regulación y Control de la *B*ioseguridad y Cuarentena para *G*alápagos; bioseguridadgalapagos.gob.ec). The ABG was established in 2012 as a technical public entity under the Ministry of the Environment of Ecuador, to increase biosecurity in the Galapagos Islands, increase operational and budgetary efficiency of allocated resources, and further advance technical capacity-building efforts. The ABG has two technical Directorates: the Directorate of Normatives and Prevention, and the Directorate of Surveillance and Quality Control for Biosecurity.

The ABG plays a central, crucial role at the interface of human, animal and wildlife health. Through multiple initiatives, the ABG prioritizes disease containment and prevention, as well as population control of domestic species. Some of these initiatives include pet identification registries, animal import/export regulatory services, disease and pest monitoring (including invasive species like Giant African Snails, introduced big-headed ants and fruit flies), disease surveillance, inspections at ports of entry, and efforts to improve the general health of agricultural and domestic species. Improved farming and disease prevention, screening, and containment practices are likely to improve efficiency and reduce the numbers of animals while still meeting agricultural demands and attempting to minimize detrimental environmental effects. Activities have included advanced training on milking practices, free dog and cat spay and neuter campaigns, deployment and training of scent detection dogs for biosecurity, and disease surveillance for livestock health (including equine babesiosis, classical swine fever, foot and mouth disease, brucellosis, and other cattle infectious diseases). The ABG has been providing support to the Galapagos National Park by conducting molecular screening of captive-raised Giant tortoises in the repatriation program to detect herpesvirus and mycoplasmal pathogens. As ABG continues to grow to fulfill its mission, a key initiative will be expanding the scope of their diagnostic capabilities and providing infrastructure for disease surveillance of domestic, peridomestic, wild and feral animals.

The Galapagos still has a policy against the importation of dogs and cats, and until recently, the use of vaccines was prohibited (Levy et al. 2008). Following a technical review and risk analysis, the regulations were updated through a resolution (Resolución D-ABG-028-03-2017) in March 2017 to allow the importation of domestic dog vaccines, specifically against canine distemper virus, canine parvovirus, canine adenovirus Type II, *Leptospira spp*., and canine hepatitis. The resolution authorizes the ABG to import, control, and apply these vaccines, and the change was partly enacted to avoid the spread of canine distemper into the native wildlife. Avoiding the introduction of risky products into the Islands has been a priority for the ABG, and the agency has expanded the availability of information through online resources to increase clarity prior to arrival, and has instituted more severe penalties when the existing regulations are not followed.

The Galapagos National Park (GNP), also under the auspices of the Ministry of the Environment of Ecuador, is responsible for protecting and preserving ecological integrity and biodiversity of the terrestrial and marine ecosystems of the Galapagos Archipelago (www.galapagos.gob.ec). Under its many strategic objectives, the GNP recognizes its complementary role in protecting the Galapagos ecosystems within the human inhabited areas. The GNP also promotes an adaptive management approach for the National Park and the Marine Reserve, based on scientific knowledge to make decisions within contexts of socioeconomic and environmental conditions of the archipelago. The GNP issues scientific permits for conducting work on the islands and ensures that disease and species introductions are properly mitigated. Under its four technical directorates (Directorate of Ecosystems, Directorate of Environmental Affairs, Directorate of Environmental Education and Social Involvement, and the Directorate of Public Use), the GNP takes a multidisciplinary approach to protecting the integrity of the Galapagos ecosystems and respective ecological processes. The GNP has set expected standards of responsible behavior by scientists conducting work in the islands in the Field Guide for Research. This guide includes existing protocols to minimize the impact of scientists and visitors in the areas, with particular interest in avoiding the introduction or spread of non-native species. It includes protocols for management and research activities, including whether these occur on land or aboard a vessel, camping in uninhabited or inhabited islands, transporting living organisms, or handling scientific specimens. Failure to comply with these protocols may result in permits being revoked, scientific activities being cancelled and even legal prosecution under the Organic Law of Special Regime of the Galapagos Province, known as LOREG for its Spanish acronym (Ley Orgánica de Régimen Especial de la Provincia de Galápagos). In 2015, LOREG was updated to be able to impose more significant economic penalties if the law is broken.

Ecuador's Ministry of the Environment is responsible for managing the Fund for Control of Invasive Species in Galapagos, or FEIG for its Spanish acronym (Fondo de Control de Especies Invasoras de Galapagos). This fund was set up from private and public donations with the intent of allocating necessary resources for implementing the control of invasive species. Recent initiatives under the fund have included the control of invasive fruit flies, the African giant snail and invasive wild berries. Implementation of various initiatives under the fund may be done by a primary agency such as the ABG or the GNP, and is usually done in collaboration with each other and local municipal government entities and support from NGOs.

The Charles Darwin Foundation (CDF) is a non-profit scientific agency registered in Belgium as an International Non-Profit Organization that has been working in the Galapagos Islands since 1959 under an agreement and in partnership with Ecuadorian government agencies to provide scientific support to conserve the Galapagos Islands. As one of the most recognizable agencies with a presence on the island, the CDF is a close partner to the GNP and a highly visible entity that welcomes and educates tourists and visitors to the islands. The CDF has its own team of scientists and has worked closely with the GNP by providing scientific support, hosting scientists, and leading scientific research initiatives. In recent years, these research initiatives have been focused on three major areas: invasive species, sustainability, and conservation management.

10.3 Threats: Hosts and Pathogens of Concern

In addition to direct effects that introduced species pose to native species, such as predation, competition for resources and modification of suitable habitat, introduced species carry the risk of disease introduction. Disease introduction is the most significant threat posed by introduced species. Establishing a baseline of the endemic pathogens of native fauna through regular disease surveillance leads to understanding the degree of existing risk for an epizootic to occur. It also leads to proactive, early detection of introduced and novel pathogens before they cause widespread morbidity or mortality. Baseline disease prevalence information is crucial to make accurate epidemiological models that could inform practical wildlife management and mitigation activities. This information, which should be frequently updated in real time, should reside with local agencies and be available to the local agencies.

The status of introduced vertebrates in the Galapagos has been described by many authors and summarized in Table 10.1. It is particularly notable that the peer-reviewed literature is limited in the documentation of diseases present in most of the agricultural species. While many authors have described the infectious disease risks of chickens (Gottdenker et al. 2005; Soos et al. 2008; Deem et al. 2012), dogs, and cats (Levy et al. 2008; Gingrich et al. 2010; Diaz et al. 2016), there is limited information on what is prevalent in cattle, goats, pigs, or equids. In recent years, the ABG has been conducting active and targeted surveillance to understand the prevalence of disease in a number of these agricultural species, and by implementing strict sanitation procedures when livestock are transported between farms, they have expanded the ability to detect disease and prevent its spread. Extensive surveillance done in cattle between 2014 and 2015 failed to show any evidence of foot and mouth disease, *Brucella abortus* or bovine leucosis virus, but did show that *Anaplasma marginale*, *Neospora caninum*, and Infectious Bovine Rhinotracheitis (IBR) virus are present at a high seroprevalence (64%, 40.1%, and 45.8% respectively). In addition, bovine viral diarrhea was detected at a 6% prevalence by serological screening (Velez 2016). This active surveillance has allowed the ABG to declare the Galapagos Islands free of food and mouth disease, and efforts are ongoing to declare them free of classical swine fever.

Regardless of taxon and the diversity of known risks that they pose to endemic wildlife and ecosystems, the biggest threat resides in the large vacuum of unknown and possible risks. Policies must be comprehensive enough that they mitigate known risks and rely on best practices to compensate for theoretical but possible risks brought by any introduced species. There are some known and possible disease risks that are dictated by taxonomic susceptibility, and although this list is by no means comprehensive, it presents the diversity of disease threats to some of the

Table 10.1 Notable species introduced to the Galapagos Islands and the risks they pose to native wildlife

Species	Risk	Pathogens Documented	Distribution	Comments
Domestic poultry (chickens, turkeys, Guinea fowl, peafowl, Asian quail)	Disease introduction and maintenance	Gottdenker et al. (2005), Soos et al. (2008)	Inhabited islands	High risk of disease introduction, transmission and maintenance for all bird species
Domestic waterfowl (ducks, geese)	Disease introduction and maintenance		Santa Cruz, San Cristóbal, Isabela	Significant risk to all bird species, seabirds and aquatic birds in particular. Strains of avian influenza may establish in domestic waterfowl
Domestic pigeons (rock doves)	Disease introduction and maintenance	Harmon et al. (1987) and Padilla et al. (2004)	Eradicated from the islands (Philips et al. 2012)	All birds susceptible to shared diseases, but in particular Galápagos doves (*Zenaida galapagoensis*) due to taxonomic relationship
Cattle egrets *(Bubulcus ibis)*	Disease maintenance Predation of native species Physical damage to mangroves, excess phosphorous and nitrogen in wetlands		Can reach all islands, breeding in mangroves and migrate to feed in agricultural grazing areas	All bird species, possible zoonotic disease reservoir (Phalen et al. 2010) Some trematodes are associated with egret species and are capable of infecting multiple species if the competent hosts are present
Smooth billed Ani *(Crotophaga ani)*	May predate native invertebrates and nestling birds May have a role in seed dispersal and in particular the invasive *Rubus niveus* berry (Guerrero and Tye 2011)		Widely distributed (see Philips et al. (2012))	Role in infectious disease transmission is unknown. Known to predate finch nestlings (Connett et al. 2013)
Red-masked parakeet *(Aratinga erythrogenys)*	Disease introduction Habitat modification		Not likely to be established	Psittacines can serve as reservoirs of *Chlamydophila psittaci*, especially if they originate from captive managed flocks or individual pets without proper biosecurity

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Table 10.1 (continued)

Species	Risk	Pathogens Documented	Distribution	Comments
Domestic cats *(Felis silvestris Catus)*	Predation of native species, Disease introduction and maintenance	Levy et al. (2008) and Deem et al. (2010b)	All inhabited islands	Cats are general, indiscriminate predators capable of impacting populations of many species *Toxoplasma gondii* is a serious protozoal parasite with an exclusively feline host known to affect a multitude of species (Dubey et al. 2003, Levy et al. 2008 and Deem et al. 2010b)
Domestic dogs (*Canis lupus familiaris*)	Predation of native species Disease introduction and maintenance	Levy et al. (2008), Gingrich et al. (2010) and Diaz et al. (2016)	All inhabited islands	Dogs can predate all species, but have impacted penguins and land and marine iguana populations (Barnett and Rudd 1983, Philips et al. 2012) *Dirofilaria immitis*, canine distemper virus, canine adenovirus, and parvovirus may be common (Levy et al. 2008) and a risk to native pinnipeds. Intestinal parasites are a risk to many species (Gingrich et al. 2010)
Donkeys and horses (*Equus asinus* and *Equus caballus*)	Habitat modification (trampling, compaction) Competition for food with native herbivores (tortoises, iguanas) Overgrazing Damage to nests by trampling Viral infectious disease introduction and maintenance	Limited published accounts	Domesticated horses are found in all inhabited islands, feral donkeys are found in Santa Cruz, Isabela and San Cristóbal (Philips et al. 2012)	Tortoise, land iguana, and ground nesting bird nests can be trampled. These species compete for food resources with the native herbivores Tortoises and other reptiles, and many bird species may be susceptible to some of the viral, arthropod-vectored encephalitides of equids

Pigs (*Sus scrofa*)	Predation of native animal and plant species Habitat modification and degradation Spread of invasive plant species and seed dispersal	Limited published accounts in peer-reviewed literature, but internal monitoring is ongoing by ABG	Santa Cruz, San Cristóbal, Isabela Floreana	Predation and tramping of nests, especially chelonian eggs and ground-nesting birds is a concern. Swine have a role in the epidemiology of zoonotic strains of avian influenza virus Efforts are underway to certify the Galapagos Islands as free of classical swine fever
Cattle (*Bos taurus*)	Habitat modification (overgrazing, tramping and compaction) Damage (collapse) of bird nest burrows Seed and plant dispersal Native plant damage Competition for food with native herbivores (tortoises, iguanas)	Limited published accounts in peer-reviewed literature, but internal monitoring is ongoing by ABG (Velez 2016)	Domesticated in Santa Cruz and Floreana, feral in Isabela and San Cristóbal	Tortoise, land iguana and ground nesting bird nests can be trampled. These species compete for food resources with the native herbivores Some ectoparasites of cattle (ticks) may affect other species, and many species are vectors for specific diseases. *Rhipicephalus microplus* ticks are common on Galapagos cattle. Serology surveillance by ABG has shown a high seroprevalence for *Anaplasma marginale*, *Neospora caninum* and infectious bovine Rhinotracheitis (IBR) (Velez 2016)
Goats *(Capra hircus)*	Habitat modification (overgrazing, tramping and compaction) Facilitate invasive, alien plants Seed and plant dispersal Native plant damage and impaired regeneration by consuming seedlings Competition for food with native herbivores (tortoises, iguanas)	Limited published accounts in peer-reviewed literature	Santa Cruz San Cristóbal Isabela	The effect of high populations of feral goats on the landscape has been one of the most well-documented environmental issues in the Galapagos, and eradication efforts have been some of the most successful programs Tortoise,land iguana and ground nesting bird nests can be trampled. These species compete for food resources with the native herbivores

(continued)

Table 10.1 (continued)

Species	Risk	Pathogens Documented	Distribution	Comments
Domestic sheep (*Ovis aries*)	Similar effects to those of goats and cattle, but not a significant issue in the Galapagos Islands		Historically farmed, not common	
House mice (*Mus musculus*)	May affect native plant mortality May contribute to seabird mortality and survival through predation (Wanless et al. 2007), or through unknown mechanisms such as disease Vectors of diseases that can affect other species		Present in at least 8 islands in the archipelago (Philips et al. 2012)	The role of mice and other rodents as disease vectors to other vertebrate species, and as agents of zoonotic diseases is well documented worldwide The use of rodenticides to control mice can have an effect on non-target species
Norway rats (*Rattus norvegicus*) and black rats (*Rattus rattus*)	Rats can be predators of the eggs and hatchlings of many species, both birds and reptiles (including seabirds and tortoises) Introduced rats compete with the native rice rats and have an effect on local populations (Harris and Macdonald 2007) Rats are disease vectors to some infectious diseases of mammals		Many islands, although they have been eradicated from several islands	Rats can predate seabird species' nests (eggs and nestlings), as well as tortoises

fauna of the Galapagos Islands. Humans have been excluded from the list, as anthropogenic effects on endemic species are much bigger in scope than the intent of this chapter. However, of particular note is the ongoing global concern of antibiotic-resistant bacteria from medical and agricultural uses emerging in wild animal populations. Animals living in closer proximity to humans are likely to share bacteria of human origin, and sometimes the exposure to antibiotics does cause a shift in internal host bacterial communities. In Galapagos, bacterial isolates from land iguanas, marine iguanas, Galapagos tortoises, and seawater suggest that living in proximity to human settlements potentially has a higher exposure to human enteric bacteria (Wheeler et al. 2012).

10.3.1 Terrestrial Mammals

There are very few native terrestrial mammals in the Galapagos and these are limited to four species of rice rats and two species of bats. Introduced rats carry a number of pathogens that can be transmitted to the endemic rice rats. In addition, all species of mammals are susceptible to rabies, a lethal virus that could be potentially introduced and spread by unvaccinated dogs or cats.

10.3.2 Marine Mammals

For purposes of this chapter, the group of marine mammals includes the 25 cetacean species (whales and dolphins) that spend their lives at sea or as oceanic migrants (within the Galapagos Marine Reserve), but also the two Otariid pinniped species that spend portions of their lives living on the coast. The Galapagos sea lion (*Zalophus californianus wollebacki*) is an endemic subspecies, while the Galapagos fur seal (*Arctocephalus galapagoensis*) is an endemic species. Pinnipeds are susceptible to a number of infectious diseases carried or transmitted by domestic carnivores (dogs and cats), including but not limited to canine distemper, rabies virus, and influenza virus. In addition, certain parasitic protozoal diseases such as *Sarcocystis neurona, Toxoplasma gondii,* and *Neospora caninum* have been recognized pathogens of marine mammals worldwide, and these are often associated with contamination of waterways from domestic carnivore feces (Dubey et al. 2003). Domestic dog feces are a source for intestinal parasites that can infect other carnivores, and have been documented in the Galapagos (Gingrich et al. 2010; Diaz et al. 2016). The presence of *Toxoplasma gondii* has been recognized in the Galapagos Islands in domestic cats and some bird species (Levy et al. 2008; Deem et al. 2010a; Verant et al. 2013), and cattle are commonly seropositive to *Neospora caninum* (Velez 2016). Although current policies prohibit the importation of dogs and cats, both species could be inadvertently introduced in ships, or illegally smuggled as companions. Dogs and cats are a risk for numerous infectious diseases, and likely serve as reservoirs for these carnivore pathogens (Levy et al. 2008). The role of both dogs and cats as infectious disease reservoirs is even more significant in the absence of vaccination programs.

10.3.3 Birds

Although no bird has become extinct in the Galapagos since the arrival of humans in 1535, the risk of disease being introduced to the Galapagos avifauna is significant, and probably of higher catastrophic potential than any other taxonomic group. Of the 152 bird species recorded in the Galapagos, 61 species are considered residents, 28 are endemic species and 16 are endemic subspecies. Sources of potential disease introduction are agricultural species (in particular poultry), migratory birds, and introduced vectors of disease (such as mosquitoes). In addition, anthropogenic environmental changes could lead to modified social interactions or variable dispersal or congregations of individuals, leading to altered disease transmission dynamics. Colonial species, most of which are seabirds nesting in clusters along shorelines, are at particular risk in the event of single environmental disasters or disease outbreaks.

Many pathogens of domestic poultry have been identified in the Galapagos Islands (Gottdenker et al. 2005; Soos et al. 2008; Deem et al. 2012) and pose an immediate concern of disease transmission if biosecurity practices are not in place. Of particular concern is the potential of Newcastle disease (avian paramyxovirus-1) becoming established in endemic, susceptible species of small population sizes, such as the Galápagos penguin (*Spheniscus mendiculus*), the flightless cormorant (*Phalacrocorax harrisi*), or the lava gull (*Larus fuliginosus*) (Gottdenker et al. 2005). Backyard poultry, where low densities of birds roam in peridomestic areas, and commercial poultry farms, where chickens are confined at high densities in a single area for a limited time until they go to market, pose significant, but different, risks of disease spillover to native wildlife (Gottdenker et al. 2005; Soos et al. 2008). On one hand, backyard poultry often roam around human settlements and may have frequent direct contact with wild birds in the peridomestic environment which may increase transmission risk, but they are at lower densities, have varying age structures, and often include long-lived genetically diverse animals in their populations that have a large amount of acquired immunity to pathogens, effectively reducing infectious disease transmission, spread, and severity. However, large-scale intensive chicken farm operations, despite biosecurity measures that attempt to reduce within-flock infectious disease transmission, consist of very high densities of single-aged, short-lived, and genetically uniform animals, which can provide a dangerous amount of susceptible epidemic fuel for pathogens with high basic reproduction numbers, creating a very high concentration of pathogens that could easily spill-over into susceptible wild species by direct or indirect contact, or vector-borne transmission. Management of poultry waste from larger scale operations is a potential concern, should such waste contain infectious agents (Gottdenker et al. 2005). *Toxoplasma gondii*, a protozoan pathogen with an obligate felid host, is one pathogen with serological evidence of exposure in Galapagos aquatic birds, and carries significant potential for mass mortalities of bird species (Deem et al. 2010a).

A well documented and impactful introduction has been the parasitic *Philornis* fly. *Philornis downsi* is an obligate dipteran bird parasite accidentally introduced to the Galapagos Islands sometime in the 1960s and documented to parasitize nestlings roughly 30 years later (Causton et al. 2013; Chap. 9, this volume). Although the adult fly has a similar lifestyle to other Muscid flies, feeding on fruit or decaying vegetation, they deposit their eggs on bird nests and the larvae parasitize nestlings. Parasitism of finches by *Philornis* larvae has been a significant contributor to the decline of some populations, in particular the endangered mangrove finch (*Camarhynchus heliobates*) (Fessl and Tebbich 2002; Koop et al. 2011). Management efforts to control the fly have proven extremely challenging, in part due to gaps in knowledge in the biology of *P. downsi*, and because the fly is widespread throughout the archipelago. A recent research initiative involving the provision of permethrin-permeated nesting material may be an effective, targeted mitigation effort (Knutie et al. 2014).

Avian malaria, the disease caused in birds by Apicomplexan blood parasites, poses a significant pathogenic threat to some of the species of endemic birds in the Galapagos. Many hemoparasites are likely to have co-evolved and co-adapted with their vertebrate hosts, but the introduction of novel parasites to non-adapted species can have extreme effects in mortality and morbidity at the population level. Competent invertebrate, blood-feeding hosts are essential to allow completion of the protozoan life cycle, transmit the parasite, and cause disease. The introduction of *Culex quinquefasciatus* to the Hawaiian Islands, and its ability to serve as a competent host to *Plasmodium relictum,* an agent of avian malaria, is recognized as a significant contributor in the extinction of a large number of endemic Hawaiian bird species (van Riper et al. 1986). Both *Culex quinquefasciatus* (Whiteman et al. 2005) and *Plasmodium sp.* (Levin et al. 2009, 2013) have been identified in the Galapagos Islands, and both are likely recent arrivals. Multiple lineages of *Plasmodium sp*. have likely entered the Galapagos via migratory birds (especially bobolinks) and not established themselves, but the possibility exists that a *Plasmodium* lineage has established itself in the islands with a local host based on its detection at multiple sites throughout multiple years (Levin et al. 2013). Unlike the situation in the Hawaiian Islands, neither morbidity nor mortality of any Galapagos bird species has been attributed to *Plasmodium sp.*, although a serological survey of Galapagos penguins showed a very high prevalence of exposure between 2004 and 2009 (Palmer et al. 2013). *Plasmodium spp.* are known potential pathogens of penguins housed under human care (Fix et al. 1988; Grim et al. 2003). It has been speculated that *C. quinquefasciatus* larvae were introduced to the Galapagos Islands in standing water on transport vessels, but it is possible that additional inadvertent introductions have occurred and may continue to occur through residual standing water within compartments in airplanes, ships, or cargo (Peck et al. 1998; Whiteman et al. 2005; Bataille et al. 2009b). This freshwater-dependent mosquito is likely to be more common around human settlements where fresh water is available, but can spread rapidly during rainy seasons (Whiteman et al. 2005) or weather events by using rain puddles.

Mosquitoes such as *C. quinquefasciatus* and *Aedes taeniorhynchus* can also be a source for introducing or spreading other arthropod-borne diseases that may enter in domestic species or be present as circulating viremias in migratory birds, including West Nile Virus, Equine Eastern and Western encephalitides (Bataille et al. 2009a). Modern trade and commerce practices pose a risk for the emergence and spread of many arhboviruses (Pfeffer and Dobler 2010). The inadvertent transport of mosquitoes in airplanes has been predicted to be the most significant risk of West Nile virus introduction to the Galapagos Islands (Kilpatrick et al. 2006), and may currently be the single most significant risk for mosquito and arthropod-borne disease introduction in general (see management response in Chap. 12, this volume). Avipoxviruses are a group of avian taxa-specific viruses that can also be transmitted by blood-feeding insects, but because the transmission is by mechanical routes, the species of mosquito is less relevant. Several avian pox strains do occur in the Galapagos (Thiel et al. 2005), and although likely to be taxa-specific, distribution patterns could be affected by the presence or absence of different arthropod vectors or changes in disease transmission dynamics caused by the various domestic animal introductions.

The Galapagos penguin, with a population of roughly 2000 individuals in a relatively limited geographic distribution, has been classified as endangered by the IUCN (IUCN 2015). Historical El Nino events have had a significant impact on population numbers: from 3000 to 699 in the 1982–1983 event, and from 2252 to 779 in the 1997–1998 event (Vargas et al. 2005). Following each reduction, the population has been slow to rebound, in part due to a low reproductive rate and high juvenile mortality (Vargas et al. 2006). The role of infectious disease during these population drops is not known. During El Nino-Southern Oscillation events, changes in oceanic currents and water temperatures lead to decreased marine productivity and less prey available to penguins. A concurrent increase in rainfall leads to optimal conditions for mosquito breeding; and some mosquitos are vectors of lethal blood parasites known to affect penguins as previously mentioned.

10.3.4 Reptiles

The Galapagos tortoise (*Geochelone elephantopus*) is probably the most iconic of the Galapagos reptiles, but is by no means the only one. Land iguanas and lizards are present on the islands, and the marine iguanas are just as unique and iconic as the tortoises for which the islands are named. A long-term Galapagos tortoise repatriation program, whereby many tortoises are raised at the breeding center in Santa Cruz Island and re-introduced to their native islands, has been successful for many years. Disease has not been considered a significant factor in the Galapagos tortoises, and little documentation exists of the diseases affecting them. Anecdotal accounts of mortality from Santa Cruz-reared tortoises has alluded to tortoises that have died of pneumonia, and infections of the intestinal or respiratory systems, but the actual pathogens have not been characterized in the published literature. Shell diseases are a common presentation in many tortoise species, and although many are superficial opportunistic problems, there are instances of aggressive fungal invasion in some species (Stringer et al. 2009). Although it is assumed that these may be opportunistic infections and common in rearing situations, further investigation of these cases would be beneficial to understand the infectious disease potential as these animals are repatriated. In any captive breeding and repatriation program, there is a theoretical risk that the breeding stock itself could serve as agents to introduce, amplify, or maintain a novel pathogen into the ecosystem. This is not a very likely risk for the Galapagos tortoise at current time and based on current knowledge, although the possibility exists for tortoises to become symptomatic from mycoplasmal or herpesviral pathogens that are thought to be enzootic in many tortoise species (Martel et al. 2009). In addition, there is a risk that tortoises could be exposed to arthropod (mosquito) vectored encephalitides, since some reptile-feeding mosquitoes have been documented in the islands and mosquitoes have played a significant role in the maintenance of viral diseases once introduced and established in some reptile populations (Unlu et al. 2010). Viruses such as West Nile virus and eastern equine encephalitis can be a threat to reptile populations, and some reptiles could even serve as significant amplifier hosts to some of these viruses (Klenk et al. 2004). As previously mentioned, air traffic is currently the most likely threat to arthropod-borne disease introduction. Introduced lizards (primarily gecko species) could serve as vectors to a number of lizard-specific viruses.

Hard-bodied ticks of the *Amblyomma* genus are known to parasitize the giant tortoises and other Galapagos reptiles (lava lizards and iguanas) (Keirans et al. 1973). There is potential for ticks to move between cattle and reptiles, and *Amblyomma spp.* are the known hosts for many diseases worldwide even if none have been recognized in Galapagos.

In recent years, fungal diseases have been identified as emerging pathogens of many wild animal species (Padilla 2011). Reptiles are no exception, and while the literature is rapidly evolving on pathogenicity and transmission dynamics of many of these organisms, significant gaps exist (Paré and Sigler 2016). This lack of knowledge of possible pathogens and their transmission dynamics warrants a conservative approach to biosecurity measures. Some mycotic pathogens are opportunistic and exploit the host's compromised immune status, concurrent infections, or an ectotherm's body temperature that favors fungal growth. However, many of the recently identified pathogens appear to be primary pathogens of ectotherm species. In many cases of fungal diseases affecting wildlife, the true nature is only recognized once the disease reaches epizootic proportions or is perceived as a zoonotic threat (Padilla 2011).

A seemingly emerging disease of epizootic potential in sea turtles is systemic coccidiosis, usually attributed to *Caryospora cheloniae*. Initially recognized in marine cultured-reared green sea turtles (Leibovitz et al. 1978), the disease has been implicated in several epizootics and mass mortality events (Gordon et al. 1993;

Chapman et al. 2016). Little is known about the epidemiology of this disease, and even the infectious organism that causes it. Recent molecular diagnostic tools should help elucidate this disease, the species of coccidia that cause it, and what are relevant risk factors to understand its transmission and protective measures to avoid it (Chapman et al. 2016). Little is known on how *Caryospora cheloniae* (or any systemic coccidia) is spread in sea turtles. Similarly, chelonian intranuclear coccidiosis is also a systemic, poorly understood coccidial disease that affects terrestrial chelonians (Garner et al. 2006).

Analysis of sea turtle eggs in other parts of the world has shown evidence of exposure to polluted effluent from humans and animal waste. (Al-Bahry et al. 2009). This is a theoretical concern with turtles around the human-inhabited islands of the Galapagos, but with the long distance migration of sea turtles it is difficult to realistically quantify how unique or impactful this could be to sea turtle populations. A survey of green sea turtle mortality in Galapagos during the 2009–2010 nesting season from three nesting beaches showed a disproportionate amount of anthropogenic interactions playing a role in mortalities (Parra et al. 2011). Interaction with fisheries and boat collisions were significant.

Fibropapillomatosis is a common proliferative disease of free-ranging sea turtles that has been seen in all species except for leatherback turtles (*Dermochelys coriacea*), although it is primarily a disease associated with green sea turtles (*Chelonia mydas*). It has a global distribution, predominantly in tropical regions. A herpesvirus is involved, but the disease is likely multi-factorial and its presentation seems to vary geographically. Environmental factors (pollution, heavy metals), host immunity and local population genetics likely influence the manifestation and spread of disease. Fibropapillomatosis is most prevalent in turtles near human inhabited shorelines, around areas with high human density and areas with degraded ecosystems, including areas affected by agricultural runoff (Aguirre and Lutz 2004).

10.4 Action Plan

Introduced species and the diseases they carry will always loom as a threat to the wildlife of the Galapagos Islands, and understanding the regulatory agencies that oversee and enforce them is crucial to the implementation of action plans aimed at protecting the native wildlife in perpetuity. The success of any conservation effort resides in the power and engagement of the local authorities and citizens who want to protect their natural heritage and make it a sustainable economic resource.

A workshop held in Santa Cruz in 2015 (Workshop Summary 2015) convened a large number of stakeholders and subject matter experts to prioritize needs and develop a logistical framework to address the current challenges. The collaboration between local agencies (including the ABG, the GNP, CDF, and other partners) is crucial. Chapter 12 describes the need and framework for local collaboration in the context of conservation. External scientists must continue to collaborate and invest in the long-term sustainability of conservation initiatives through in-country capacity building.

The 2015 workshop group identified seven main priorities, of which some action plans are already being implemented.

10.4.1 Priority 1

Establish an adequately staffed, equipped, and biosecure laboratory facility that can quickly diagnose, detect, and maintain diseases in real time. Secure, sustainable, and long-term operational funding is essential for this priority to have the intended effect. This facility would be basically equipped for diagnostic services in clinical pathology and microscopy, molecular biology, parasitology, microbiology, serology assays, and general pathology. A local diagnostic lab would improve the turnaround time to get results for disease investigation and surveillance, as well as for quarantine and biosecurity maintenance. The ABG is a logical agency to take the leadership on such a diagnostic facility.

A secondary goal would be to incorporate a facility that allows for clinical management, treatment, and better understanding of disease syndromes affecting individual animals. For such a facility to be truly impactful, procedures must be in place to keep track of disease trends and diagnoses. The facility must remain true to the priority of a wildlife disease and detection facility, staffed by trained and competent veterinarians and diagnosticians, or could be at risk of becoming a permanent holding facility for individual animals with irreversible conditions that render them non-releasable and become an undue burden on local resources.

10.4.2 Priority 2

Establish and refine wildlife health program policies and procedures. This initiative would include reviewing policies on domestic animal vaccination protocols and products used and reviewing and reinforcing policies for the prevention of entry of diseases in human-habituated islands. It would also include policies for preventing disease occurrence and altering host-parasite evolution, continued disease surveillance and developing emergency contingency plans to respond to unusual morbidity and mortality events.

Management policies in the Galapagos Islands should be continuously evaluated to critically determine if they are having the intended effect on overall health management and species conservation. A praiseworthy example is the aforementioned resolution (D-ABG-028-03-2017) signed into effect in March 2017 that allows the importation and use of domestic dog vaccines against significant canine pathogens. Prior to that, the policies prohibited all animal vaccinations in Galapagos. This policy was in place to contain the possibility of vaccine-related disease introduction from modified live strains, and may serve a diagnostic purpose in serological pathogen detection through surveillance efforts. A scientific technical review and risk analysis done in late 2016 led to a revision of the policy for domestic dogs through the newly enacted resolution, although it is still in effect for other species. As vaccine technology has advanced and safer vaccines are available, vaccines can be a barrier to prevent disease spread. In the absence of robust vaccination programs, susceptible animals that are already infected with infectious diseases may serve as a reservoir for maintaining the disease (Levy et al. 2008). The process that led to the ability to import and use canine vaccines is a model that can be used for all species: infectious disease surveillance led to a refined definition of perceived need, followed by a technical review and risk analysis, which was then put into action to halt the spread of high risk pathogens. Although it is possible that domestic dog vaccines had been used illegally in the past (Diaz et al. 2016), the regulation of vaccine products through the ABG will allow this to be a part of a comprehensive disease control, prevention, and monitoring strategy.

Currently, air travel into the Galapagos Islands must originate in either Quito or Guayaquil. These flights undergo appropriate inspection and disinfection to curb introduction of agents of concern (*see* Chap. 12, this volume). However, the bulk of cargo enters the islands by sea, and these ships undergo inconsistent methods of inspection and disinfection. Standardization of policies and continuity in how the knowledge is preserved and passed during staff changes is essential for this initiative to be fruitful. Without the needed continuity and consistency, the policies would be at risk of being exercises on paper that do not have a functional application.

Support should be in place to promote the science-based policies among the public and local residents through education and public relations campaigns. For example, a recent study has shown that despite successful dog sterilization campaigns implemented in Galapagos, the dog population in Santa Cruz island is higher than predicted, and it is believed that the local culture against surgically sterilizing dogs is a limiting factor to effectively control populations (Diaz et al. 2016). In cases such as these, enforcement of the policies could even be incentivized to promote acceptance and advance implementation.

10.4.3 Priority 3

Continue to invest in capacity building, technology advancement and continuity of knowledge and local expertise in animal health. This priority for capacity building and continuity of knowledge is crucial to everything else in any action plan. If technical expertise and knowledge leaves, the technology transfers become obsolete pieces of equipment. The scientific staff must be continually connected with scientific advances worldwide (*see* Capacity Building, Chap. 12 this volume). Technology transfer with limited transfer of expertise or continuity of expertise is a common hurdle that plagues many well-meaning but eventually unsuccessful conservation initiatives.

10.4.4 Priority 4

Establishment of a rehabilitation facility for treatment of chronically injured or diseased animals. For a rehabilitation facility to be successful the organization must have clear goals, triage, and resource prioritization decision trees, or they will be overwhelmed by the constant influx of injured or diseased individuals who could become permanent residents.

10.4.5 Priority 5

Develop a centralized data management platform that is easily accessible to all stakeholders. Access to data, in real time, is important to have the necessary objective information to implement wildlife management and policy decisions. If surveillance information is being generated through a diagnostic laboratory on site, this could simplify the number of steps and connections before the information comes back to Galapagos. There must be transparency and collaboration, and avoid the pitfalls of secrecy and individual territoriality over pet projects.

10.4.6 Priority 6

Standardize protocols to maximize the value of health-related information collected from live animals. Standardized protocols are useful for mining data and extracting epidemiological information. This is important to take full advantage of situations as they present themselves. Perhaps equally important is the continued training of on-site personnel for clinical problem-solving and health diagnostic approaches to rule in or rule out diseases of concern, and should be done in conjunction with Priority 3.

10.4.7 Priority 7

Establish a facility or relationship with an existing facility that will serve as a repository of all biological samples collected in the Galapagos Islands. Proper curation of all samples from the Galapagos should take place so that the samples are in one protected place as the property of the Ecuadorian government. If a new pathogen is detected in Galapagos, such a repository could allow agencies to “look back” and test previously collected samples to determine when and where that pathogen first showed up in historic samples.

The Galapagos Islands will always continue to be a unique biological resource and a prime ecotourism destination. The future is bright, with strong initiatives and engagement from local scientists and support from many partners. Animals—domestic, peridomestic, and wild, will continue to be present in the islands. The management of introduced species and surveillance for diseases that could be introduced are key components of protecting the Galapagos fauna in perpetuity.

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Chapter 11
Filling the Gaps: Improving Sampling and Analysis of Disease Surveillance Data in Galápagos

Kathryn P. Huyvaert

Abstract Emerging infectious diseases in wildlife are of conservation concern worldwide, including on the Galápagos Archipelago, where isolation, small population sizes, and naïve immune systems place the birds of Galápagos at potentially higher risk of devastating impacts of disease. Wildlife disease data from surveillance efforts, whether active or passive, are invaluable because they provide a baseline understanding of what diseases are present in a system, serve as an early warning sign of an ecosystem health issue, and provide managers with information about the efficacy of disease mitigation efforts. We have learned an enormous amount about diseases affecting Galápagos avifauna in the last 20 years or so, but gaps in our understanding exist because of the challenges posed by issues with imperfect detection of hosts, parasites and pathogens, and the diseases they cause as well as uncertainty about the size of the population of the target host. Nonetheless, sampling design and analytical approaches borrowed from population and community ecology offer a suite of tools to help fill the gaps in our knowledge about diseases in wildlife in Galápagos and beyond.

Keywords Detection probability • Occupancy models • Wildlife disease surveillance • Dependent double-observer method • False positive

11.1 The Values of Wildlife Disease Surveillance Data

Emerging infectious diseases (EIDs) are an important threat to wildlife as disease contributes to changes in system dynamics at multiple scales. Work on emerging diseases in the avifauna of the Galápagos Archipelago over the last two decades, as detailed in this volume, illustrates well the impact disease has at these different

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layers of organization. *Philornis downsi*'s devastating influence on nestling survival in Darwin's finches (Fessl et al. 2006a, Chap. 9, this volume) will likely reverberate from the individual host nest that is affected, up through island populations of these iconic passerines. Disease resonates to higher scales, as well. The discovery of antibodies to *Toxoplasma gondii* in endemic Galápagos Penguins (*Spheniscus mendiculus*) and Flightless Cormorants (*Phalacrocorax harrisi*) on both islands with and without felid definitive hosts (Deem et al. 2010, Chap. 8, this volume) highlights pathogen transmission as yet another negative impact feral cats can have on bird communities. Further, while largely ubiquitous across the globe (Dubey 2009), the presence of *T. gondii* in an isolated system like Galápagos might serve to signal a potential public health issue (Levy et al. 2008) reflecting an ecosystem that is not as "healthy" as we might wish.

Despite recognition of these impacts echoing throughout wildlife host-parasite-environment systems, important challenges remain in part because wildlife disease management at all stages—from the initial incursion of the pathogen to its possible elimination—often lacks relevant or sufficient data (McCallum 2016) or appropriate management actions (Langwig et al. 2015). After highlighting the values of health survey data in the context of the avifauna of the Galápagos, my goals for this chapter are twofold. One goal is to describe some of the challenges posed by wild systems that lead to gaps in data collection and analysis needed to fully characterize the complex interactions and dynamics of disease in wildlife systems (McClintock et al. 2010). The second is to describe approaches for data collection and analysis—borrowed from population and community ecology—to address the gaps in our knowledge about these critically important wildlife diseases.

Disease surveillance comprises the systematic and ongoing collection and analysis of health data (Toma et al. 1999) which, in our case, pertains to infectious diseases in wildlife with the eventual application to wildlife disease management. Ryser-deGiorgis (2013) nicely captured the goal of wildlife disease surveillance as gathering "information for action." The principal roles such disease surveillance data play are: (a) as a catalog of the diseases affecting hosts and the pathogens or parasites that cause them; and (b) as a long-term record of changes in host population disease status over time. Initial questions are often "What is present and whom does it affect?" and many of the early papers on disease in birds in Galápagos provide the baseline for future work tackling deeper questions that could not be addressed had the baseline not been established. Avian pox in the Waved Albatross (*Phoebastria irrorata*) presents a good example. Initial detection of external, wart-like gross lesions (Tompkins et al. 2017) like those characteristic of "dry" cutaneous pox infection (Tripathy 1993) is typically high. Detection of the lesions triggers tissue sampling to confirm by histopathology and electron microscopy (i.e., presence of inclusion bodies) or molecular methods (Tripathy 1993) that the lesions were caused by an avipoxvirus and not another agent. In addition, previous reports of active or targeted disease surveillance (Ryser-Degiorgis 2013) in the same or related host taxa, like Galápagos seabirds (Padilla et al. 2003, Padilla et al. 2006) in the albatross case, must be checked to confirm whether pox had been seen in these hosts in the past; in this case, we know that the virus has been present in Galápagos for at least a century (Parker et al. 2011), but never previously reported in the Waved Albatross. This work then forms the foundation for continued surveillance for disease as a factor contributing to changes in the status of this critically endangered seabird.

Passive or scanning surveillance takes place as incidents of disease occur (Ryser-Degiorgis 2013). Such opportunistic surveys present some issues with respect to detection because the sample is not designed to represent a target population, but such surveillance data provide another important stream of information to document "What is present?" The advantages of passive surveillance arise from the broad scope covered by the survey in terms of host distribution and causes of morbidity or mortality. For example, passive surveillance efforts using submission of dead birds for necropsy in Galápagos (Gottdenker et al. 2008) included findings from 28 different species in 9 different avian orders and representing 10 different causes of mortality. Incidental findings included reports of cutaneous lesions consistent with avian pox, including in an Audubon's Seawater (*Puffinus lherminieri*); these are all discoveries that would never have been made had the authors not taken advantage of the opportunity presented by the carcass submissions.

Both active and passive surveillance data serve the critically important role as an early warning sign of a potential conservation threat; this is particularly germane to the Galápagos where populations are isolated, small, and likely immunologically naïve to introduced pathogens (Wikelski et al. 2004). Reports of antibodies to *Toxoplasma gondii* in Galápagos Penguins (Deem et al. 2010; Chap. 8, this volume) illustrate the utility of a sentinel species. Penguins interface with both the terrestrial and marine environments for nesting and foraging, respectively, such that they can experience stressors from both environments and track changing conditions in both environments in a way similar to sea turtles (Aguirre and Lutz 2004). Coupled with their response to the changing environmental conditions, changes in the incidence of disease in the sentinel species may reflect human-induced environmental change indicating an emerging threat to ecosystem health (Newman et al. 2007).

Lastly, surveillance data are valuable for tracking the efficacy of disease management activities when collected before, during, and following a disease management intervention. These monitoring data track changes to the host population disease status and can be used to evaluate the prediction that the intervention contributes to declines in disease incidence or prevalence. Infestation of nests with the parasitic larvae of the fly *Philornis downsi* has been connected to the declines of at least two finch species in Galápagos (Fessl et al. 2006b; Chap. 9, this volume), including the critically endangered Mangrove Finch (*Camarhynchus heliobates*). Population viability analyses suggested that reducing parasite prevalence would lead to important reductions in the risk of finch extinction (Koop et al. 2016), a hypothesis that could be tested with an active intervention to reduce infestation and the effectiveness tracked by disease surveillance to see if the intervention contributed to declines in fly infestation in finches.

11.2 Challenges Studying Disease in Wild Systems

So much of what we know about disease in Galápagos avifauna has come from the proverbial "blood, sweat, and tears" and much has been learned from this very hard work, perseverance, and a dash of serendipity. Indeed, as the contributors to this volume will attest, collecting surveillance data on disease in the field can be expensive and the logistical challenges are sometimes intractable. Nonetheless, several additional challenges to effective disease data collection are posed by the very nature of the system. A first challenge in studying disease in wild systems is that detection is imperfect (McClintock et al. 2010). Given their long isolation, island host populations tend to be relatively smaller and have lower genetic variation than their mainland counterparts (Chap. 4 this volume, Frankham 1996). Sources of uncertainty in detecting disease in wild birds might then arise, first, because host populations are small and the density of occurrences of disease may be concomitantly small and difficult to detect.

Host status further complicates detection of the incidence of disease and estimates of prevalence. Sick animals may behave differently than healthy conspecifics, making their detection more or less difficult and this leads to biased estimates of prevalence. Hunter harvest of mule deer with chronic wasting disease (CWD) increased over the course of a hunting season perhaps because they were more susceptible to harvest due to behavioral changes associated with disease. This differential susceptibility to harvest, the authors speculate, may have led to estimates of CWD prevalence that were biased high (Conner et al. 2000). House Finches (*Carpodacus mexicanus*) experimentally inoculated with the bacterium *Mycoplasma gallisepticum* exhibited more "sickness behaviors" (e.g., lethargy) than uninoculated individuals (Love et al. 2016); in a field setting, changes in behavior due to disease could translate to lower capture probabilities—infected birds are not captured in mist nets—and attendant lower detection of diseased birds.

Another issue relates to the actual size of the host population affected. Prevalence is typically calculated as the proportion of the sample examined that is classified as infected or "diseased" and this proportion is assumed to represent the true population prevalence. Often, estimates of prevalence are limited to the small subset of the population that is actually sampled, which is likely limited by the resources available for field sampling and subsequent analysis, without knowledge of the size of the total population the sample represents. This is likely unimportant when host population size is stable, as in many populations of domestic animals, but not accounting for fluctuations in wildlife population size and disease prevalence over time can lead to surveillance efforts that do not provide an effective assessment of disease risk (Walton et al. 2016) in what may be a very vulnerable wildlife population.

Imperfect detection of disease in wild systems may also arise because of issues related to the test or assay used to detect the parasite, pathogen, or disease itself. Prominent among the issues with tests used to detect parasites and the disease they cause is that many assays have been developed using well-understood domestic animal models, like domestic chickens, and then applied to a phylogenetically closely related wild organism (Pedersen and Babayan 2011). In particular, the issue is that the wild host's immune response likely does not parallel that of the domestic analog; the wild organism's immune response occurs under natural conditions and in the face of natural genetic variation (Pedersen and Babayan 2011). In many but not all cases, application of domestic animal assays to the immune response of a wild organism can result in low test sensitivity, because the test is not very good at detecting disease in a non-target host, and concomitant false negatives. False negatives are problematic in the context of Galápagos and other sensitive avifauna if management decisions are made based on the results of the assay used to detect disease: scarce financial resources may be committed to other projects when they are urgently needed to mitigate a disease outbreak that goes undetected. This urgency is compounded when a novel and virulent pathogen arrives in the archipelago, rapidly becomes established, and spreads among immunologically naïve hosts. The challenge is in detecting the incursion before rapid transmission and deleterious effects on hosts occur.

We can look to the tests used to detect infection with avian blood parasites as a case study illustrating the issues that arise when tests are not sufficiently sensitive to detect parasites or the diseases they cause. Infections with protozoan blood parasites in the genera *Haemoproteus*, *Plasmodium*, and *Leucocytozoon* are typically identified using microscopy to examine thin blood smears or by polymerase chain reaction (PCR) and sequencing, to confirm the presence of parasite DNA in a peripheral blood sample from a bird. Work by Fallon et al. (2003) showed that detection of avian blood parasites from the genera *Plasmodium* and *Haemoproteus* was different for microscopy compared to three different PCR-based assays (i.e., three different primer sets) and none of the assays alone detected all infections. *Plasmodium* blood parasites have been detected in at least 4 Galápagos bird species so far out of 22 tested (Levin et al. 2013) and we know from Hawaii that the impacts of *Plasmodium* infection on host populations can be devastating, contributing to the declines and extinction of many Hawaiian forest bird species (van Riper et al. 1986). Given this, imperfect detection of the parasite or the disease can have profound consequences for disease management because a missed detection of this sort of parasite could lead to rapid spread without our knowing.

A related but distinct issue may be more prominent in Galápagos than in other settings. Detection of *Plasmodium* in the Archipelago is thought to be poor in endemic species like the Galápagos Penguin because they do not appear to be competent hosts for the *Plasmodium* Lineage A. Gametocytes detected in host erythrocytes indicate the final stage in the completion of the portion of the life cycle that takes place in the vertebrate host, meaning that that host species is a competent host (Valkiunas 2005), but gametocytes have never been documented in any species of infected endemic bird in Galápagos (Levin et al. 2013). Two types of early intraerythrocytic development (meronts and trophozoites) have been observed in blood smears and the working hypothesis is that the host and parasite are poorly adapted to each other, as may happen when hosts and parasites have co-occurred for only a short time. Thus, by applying typical blood parasite PCR assays to blood samples, many infections likely remain undetected, and the "gold standard" microscopic inspection of thin blood smears is even worse at detecting existing infections.

11.3 Tools for Enhancing the Study of Wildlife Disease

To tackle the variety of challenges I have detailed related to evaluating the dynamics of wild host-pathogen-environment systems, we can borrow sampling designs and analytical approaches from population and community ecology that recognize—and allow us to account for—variation in detection probabilities of hosts, parasites, and the diseases they can cause. Several excellent works provide extensive detail on the development of these approaches (e.g., Jennelle et al. 2007, Conn and Cooch 2009, McClintock et al. 2010); my intent is to provide an overview that will allow workers to identify useful new approaches to apply to surveillance in their wildlife disease systems.

11.3.1 Accounting for Imperfect Detection

When the probability of detecting a target species, whether a host or parasite, is <1.0, it is “imperfect”; estimates of parameters like abundance or prevalence that use counts of the target species will be biased low when detection is assumed to be perfect (Cooch et al. 2012). Helpfully, many approaches exist that acknowledge that detection of a target species can be imperfect; that is, false negatives can occur. Occupancy modeling presents one approach where uncertainty in detection can be evaluated by making repeated visits to a site during which the presence or absence of the species of interest is recorded as a “1” or “0,” respectively. The repeated visits to the site are collated into an encounter history, recorded as a series of 1s or 0s indicating the state of the species at each sequential visit to the site, and maximum likelihood methods are used to estimate the probability of detection (p) and the probability that the site is occupied, or sometimes “used,” by the species of interest (ψ) (MacKenzie et al. 2006).

In a disease setting, the target species could be the host, the pathogen/parasite, or both, and occupancy approaches are finding increasingly widespread use with applications to hosts, parasites, and the tests used to evaluate disease status (arguably the interface of a host and a parasite). For example, multi-state occupancy approaches have been applied to arctic-nesting geese and *Toxoplasma gondii* (Elmore et al. 2014), a pathogen that has also been detected in cats in Galápagos (Levy et al. 2008) as well as some vulnerable Galápagos seabird species (Deem et al. 2010). In the arctic goose example, the risk of transmission to other potential hosts in the ecosystem, as well as to humans through harvest for consumption, motivated the need for reliable estimates of seroprevalence in geese. Estimates of seroprevalence under an occupancy framework were compared to naïve estimates that assumed that the diagnostic tests were error-free, a strong assumption, particularly in wild systems where the arsenal of tools available is absent or limited to phylogenetically similar laboratory analogs (Pedersen and Babayan 2011). Estimates of seroprevalence under an occupancy framework were ~10% higher than those using a traditional estimator of prevalence (Elmore et al. 2014). Further, the occupancy approach revealed important differences between two available serological tests where one (Indirect Fluorescent Antibody Test, IFAT) had a higher probability of detecting antibodies and a higher probability of classifying a positive sample as positive than the other (Direct Agglutination Test, DAT), given that the antibodies were present (Elmore et al. 2014). Taken together, these results emphasize that an occupancy approach could be particularly useful in surveillance of wildlife disease systems where a positive test result at some point in time could indicate a serious threat to the conservation of an iconic species.

Applications of occupancy models have recently been extended far beyond the serosurvey to include the analysis of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* in eDNA (water) samples (Schmidt et al. 2013), fleas on prairie dogs (Eads et al. 2013), and *Borrelia* in ticks infesting seabirds (Gomez-Diaz et al. 2010), among others. In all of these instances, inferences about the disease system were improved by making multiple “visits” to a target host, site, or sample to account for imperfect detection inherent in these wild systems. Further, later visits to focal or study sites in subsequent seasons or years can be appended to the encounter histories and incorporated into updated analyses as necessary for long-term surveillance. Thus, I echo McClintock et al. (2010) that occupancy approaches are so valuable because they allow researchers to account for the imperfect detection inherent in wildlife host-parasite-environment systems and advance our understanding of the dynamics and consequences of disease in wild populations, getting us one step closer to closing gaps in our knowledge.

11.3.2 Estimating Population Size

It is a rare case when every animal is detected and perhaps it is rarer still when the detection probability for both infected and uninfected animals is the same and equals 1.0. In challenging field settings, we tend to be limited by opportunity or resources to only those few animals that we can sample easily; inferences suffer when we assume that we are perfect at detecting all types of animals and when we extrapolate information about a small sample to a much larger and unknown population. When host population size is unknown, the extent of disease risk is also, arguably, unknown.

We can do better by estimating population size directly. A number of techniques exist for estimating population size (Williams et al. 2002); I highlight a few here that I think could be useful in improving our understanding of disease in Galápagos avifauna though their utility is certainly not limited to just this setting. An option that is especially attractive for use in field settings like Galápagos is the double-observer method detailed by Nichols et al. (2000). The method was initially described for use in (avian) point counts to estimate the probability of detection and sources of variation in detection, such as those that arise because of differences among bird species or observers doing the counts. In practice, the method requires two observers, a primary and a secondary. The primary observer indicates to the secondary target individuals that should be tallied. The secondary observer records the number of those indicated by the primary observer while also recording any additional individuals that the primary does not detect. Key to the application considered here is that the information on the numbers of birds not detected by the primary is used to estimate abundance (Nichols et al. 2000).

Data collected using this dependent double-observer protocol can then be summarized as individual encounter histories where observation by the two observers functions as two separate encounters. For instance, those animals seen by the primary observer would have an encounter history of "10" and those seen by just the secondary have an encounter history of "01." Using a Huggins closed captures model (Huggins 1989, 1991), like those implemented in Program MARK (White and Burnham 1999), we can get estimates of detection probability (p), we can evaluate competing hypotheses, or models, incorporating covariates to explain heterogeneity in detection (like that between observers or sites or timing of the survey, etc.), and we can obtain estimates of abundance ($\hat{N}$). Double-observer methods have been applied to estimate population size of blue-footed boobies in Galápagos (Anchundia et al. 2014) but disease-related applications have not yet been explored. It is especially appealing that this approach can be extended to counts—and therefore estimates of abundance—of individuals in different states as might be germane for estimating the abundance of classes of birds with and without ectoparasites, for example, or other syndrome with readily observed external signs. Though I have not seen applications of this sort, a dependent double-observer protocol also could be applied to microscopic evaluation of thin blood smears to estimate abundance of particular cell types like different stages of intraerythrocytic parasites such as *Plasmodium*.

Capture-mark-recapture approaches are useful when estimates of vital rate parameters like survival and population rate of change (λ) are also of interest. These time, effort, and cost-intensive methods require marking or banding a portion of the population initially, then revisiting the marked individuals by observing or by capturing them again to read their unique band numbers. Encounter histories are built from the series of encounters with the marked individuals over time in the same way that encounter histories were developed for occupancy and double-observer approaches. The relevant time steps—days, weeks, months, or seasons—for reencountering the marked animals will depend on the question of interest. Importantly, variables such as disease status, age, sex, or other individual covariates can be collected at the same time and incorporated into models of detection probability (p) and the vital rates of interest (e.g., survival). Mark-recapture models incorporating disease status have been used to document improving survival of little brown bats in the face of white-nose syndrome (Maslo et al. 2015) and to track the impacts of avipoxvirus infection on great tits (Lachish et al. 2012), among others. Occasionally, information about an individual is ambiguous—such as disease state—and one way of handling ambiguous states is to censor those data at the expense of precision of the estimates of parameters of interest such as the rate of transition from, say, a diseased state to a not-diseased state. Multi-state capture-recapture models using a hidden Markov process (Conn and Cooch 2009) offer an approach to estimate state transition probabilities and survival in the face of uncertain classification of disease states.

11.4 Parting Thoughts

Emerging infectious diseases are increasing globally for humans, domestic animals, and wildlife alike (Tompkins et al. 2015); they pose a critical conservation concern for many wildlife species. In Galápagos, we have learned a great deal about the diseases affecting wild bird populations, yet gaps in our knowledge about disease persist because of challenges posed by elements of this wild system. I have described some approaches borrowed from, but not exclusive to, population and community ecology. At the same time, here I add a few parting thoughts to make the most of these approaches should they be amenable to another wildlife disease surveillance application.

While a number of excellent works exist that describe these methods in detail, freely available software with online guides exist for all of the approaches described. Prominent among them is Program Mark (White and Burnham 1999, http://www.phidot.org/software/mark/) which has a robust user's forum (http://www.phidot.org/forum/index.php), a "gentle" online book introducing the growing list of model types and how to implement them in MARK (http://www.phidot.org/software/mark/docs/book/), and workshops are offered frequently. Occupancy models can also be implemented in Program PRESENCE (MacKenzie et al. 2006) and PRESENCE can be called from R (http://cran.r-project.org/). The R package RMark is also available for mark-recapture analyses for those who are accustomed to the R environment.

The focus of the discussion presented here has been on the empirical components—study design, data collection, and analysis—of a discovery process in which mathematical models have important roles at all steps (Restif et al. 2012). I suggest that transdisciplinary collaborations with modelers, empiricists, and those whose expertise are in the field and the laboratory will bear important fruit for wildlife disease management (Chap. 12 this volume). Moreover, just as we can borrow approaches initially described by population and community ecology, we can learn a good deal by sharing ideas across the discipline of wildlife disease management with disease ecology theory to maximize learning about both enterprises (Joseph et al. 2013).

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Chapter 12
Collaboration and the Politics of Conservation

Patricia G. Parker, R. Eric Miller, and Simon J. Goodman

Abstract Todays world is a complicated place, and it is difficult to imagine a meaningful conservation effort that will not require positive interactions among people of different backgrounds. At the very least this will include scientists from different areas of expertise, field naturalists, and policy-makers, often from different countries, different social expectations, and speaking different languages. Often additional requirements are included in the mix. In this chapter, we will discuss the changing world of how science is done, including conservation science, why collaboration is necessary, and how to approach a collaborator to enhance the likelihood of success. We will focus particularly on efforts to impact management decisions in the Galapagos Islands, and what may make this a less daunting challenge than elsewhere, but what challenges are present despite the focus of multiple Galapagos agencies on conservation. We focus on the nature of our collaborations with Galapagos agencies, and the critical importance of building stable local capacity in a changing political environment.

Keywords Scientific collaboration • Conservation • Cooperation • Conservation and management

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12.1 Collaboration

12.1.1 The Changing Face of How Science Is Done

Effective conservation cannot be done by scientists alone. At the very least, it requires communication among scientists and government officials who are charged with creating and enforcing management policy for safeguarding wildlife populations. But it likely involves layers beyond these two, as there are frequently complex logistical tasks requiring special expertise, accountants who monitor funding decisions, and one or more bureaucracies involved in procurement and oversight (e.g., Podesta et al. 2013). In this chapter, we will discuss the role of collaboration in conservation, beginning with the science itself.

Science has become increasingly collaborative over the last 20 years. This is due to a number of factors, including the increasing acceptance of English as the universal language of science (it was German when PP was in college!), and the ease of communication through electronic media. These are factors that make collaboration *possible*, but what makes it *desirable* is that technological approaches have radiated into new and diverse perspectives that are rarely mastered by a single person or even a single research group. Thus, to mount a robust approach to a problem in wildlife conservation, cooperating teams with different skill sets can put together a synthetic approach not possible for a single researcher or research group. The rapid increase in international science collaborations has been studied as an epiphenomenon unrelated to its cause, with conclusions that some countries are particularly well represented in international collaborative work; a more interesting resulting pattern is that the "rules of engagement" in collaboration arise from the individual collaborators and are not imposed by any regulatory oversight agency (Leydesdorff and Wagner 2008).

Good science constructs alternative hypotheses and then attempts to reject them. If a wildlife population is in decline, a meaningful approach is to consider multiple causes for the decline, rather than just the particular approach of the focal research group. For example, if vermilion flycatchers are in decline on San Cristobal (in fact they appear to be gone now from that island), one might have wanted to know about disease prevalence on that island. However, other factors may also cause decline, such as habitat destruction, or a new predator or competition with an introduced species. If one found a pathogen in stored blood samples from this now-missing population, that would not confirm that pathogen as the cause of their disappearance; it simply confirms the former presence of both the bird and the pathogen. In this case, alternative hypotheses that could be considered are that (1) the pathogen was the primary cause of decline, or (2) it is secondary, and weakened individual animals so that they became susceptible to other stressors, or (3) it is incidental, meaning that it has no effect on the animal's health. A robust approach would consider multiple possible causes simultaneously and assemble the appropriate expertise to evaluate the contribution of each.

12.1.2 Recognizing Reciprocal Needs

Good collaborators recognize that they need each other for success. Collaborators bring essential skills and access to the elements necessary for the work to go forward. An analogy could be fitting together the pieces of a puzzle that are needed to make the whole. That may include access to personnel with or without special expertise—sometimes even untrained helpers are exactly what is needed. At times, local collaborators can provide access to sites not available to foreign nationals, and the foreign nationals may have additional expertise or funding; whatever the distribution of financial, technical, or personnel resources, reciprocal need can provide a foundation for strong collaborations. Conservation scientists need the attention and interests of policy-makers to apply their findings in meaningful ways, and management policy-makers need conservation scientists to help them make the right management choices.

12.1.3 Reciprocal Respect

Good collaborators respect each other. Care must be taken to address reciprocal roles and needs as an equal exchange—care must be taken that it is never patronizing in either direction. Whether the respect stems from the recognition of status of a collaborator or the mutual need of collaborators is largely irrelevant. The surest way to ruin a collaboration is to walk into it assuming that you yourself are providing the most important, most challenging, or most impressive part of the joint work. The fact is that you need each other, and a better approach is to assume that what each partner brings to the table is just as important or impressive as what you bring. Values differ among institutions: in our own example, the primary academic institution (UMSL) holds peer-reviewed publications as the most valued currency of success. The other partners have different value structures. The Saint Louis Zoo values the publications, but also the visibility of being seen to be doing important conservation work in a site as iconic for wildlife as the Galapagos Islands. Like many zoos around the world, their priorities go well beyond species in human care, to include understanding and protecting animals in the wild. They are funded largely by private donations, and so this visibility is important to them. The Galapagos National Park wants the information and management recommendations: what should they be worrying about with respect to disease and what can they do about it? The Charles Darwin Foundation is also funded by private donations, and their mission is to assist the Galapagos National Park in their wildlife conservation mission. So they appreciate the publications, but value most the information and the visibility. Most of the values are shared across the collaborating institutions, but the relative emphasis of each differs strongly among collaborating institutions. Recognizing these fundamental differences in institutional priorities may help in developing respectful approaches to other institutions in collaborations. But regardless of the different value structures, all partners should receive their share of the currencies of success, whether credit in the form of authorship, visibility in the form of public recognition, and of course the information resulting from the partnership (see Sect. 12.1.6 on Credit and Acknowledgment).

12.1.4 Agreeing on Roles and Levels of Participation

It is important to agree ahead of time on the objectives of any collaborative effort. In Galapagos, we have worked under a series of 5-year Memoranda of Understanding (MOUs). Each declares the joint interests of the partners in understanding disease threats to Galapagos birds, and specifies what each partner will provide to the collective work, as well as any restrictions on what can be offered. The MOU has an escape clause in case the work is not proceeding according to the plan, whereby any party can withdraw from the agreement without penalty. This kind of formal oversight may be helpful in situations where government turnover requires a formal agreement so that the work is not abandoned by one party because they were simply unaware of it. Agreements between scientific collaborators may not require this level of formality, but some kind of expression of mutual understanding is helpful at the beginning of any collaboration.

Prior written agreement also helps avoid the pitfalls of misconceptions about what a "collaboration" means to the different parties. On one occasion of renewal of our 5-year MOU with Galapagos partners (the Galapagos National Park and the Charles Darwin Foundation), the then-Director of the Park wanted a clause stating that they would be coauthors on all publications resulting from the collaborative work. PP would not agree to this in our formal MOU unless they were willing to guarantee their ability to participate at a level deserving of authorship (see Sect. 12.1.6 on Credit and Acknowledgment below). At that time, the Park, while formally attesting to their interests in understanding disease ecology of Galapagos wildlife, committed only to waiving certain permit fees and facilitating rapid processing of annual permits. While we certainly appreciated their commitment and this kind of facilitation, PP wrote to them that we welcomed their further involvement at a level that would deserve coauthorship, and we would guarantee coauthorship when these criteria were met, but would not guarantee coauthorship as part of the 5-year MOU. They accepted this.

12.1.5 Communication—Routine and Consistent

Regular communication among collaborating partners is essential to smooth progress. This has been one of the most challenging aspects of managing a multinational multi-institutional collaboration. As the collaboration grows, the number of partners at different levels expands. For example, we have involved a number of international experts in our work, particularly when focusing on pathogens that are revealed in our surveys but with which we have little experience. And even when we develop our own expertise with a particular pathogen, it is always helpful to continue to receive input from an international expert who is recognized as a "world expert" in a particular area or a particular taxonomic group. With this expansion, regular communication with ongoing partners can become challenging as the number of people involved grows. Further, there may be particular contact personnel with whom the logistical communications occur, and one can never be sure that these contacts, even when they are very effective at their jobs, are communicating with their own superiors within the organization. Turnover at all levels further multiplies the challenge. When a language barrier exists, the time commitment required for effective communication grows. Good communication is an aspiration, an objective we consistently try to improve.

12.1.6 Credit and Acknowledgment

The sharing of credit is perhaps the most critical currency in a successful collaboration. Some might argue that funding is the critical currency to begin the work, but sharing of credit from the outset is critical to continuing a successful collaboration. Even recognizing that the value structure of institutions differs, each should be given public credit for their work in all currencies of credit, when they are deserved. That is, one cannot deny authorship to a deserving participant because of our understanding that authorship is not valued as highly by their institution as it may be in an academic institution: if they meet the criteria for authorship, they should be offered authorship. A similar argument has been made for paid assistants versus unpaid assistants, as if the financial compensation is the paid participant's reward and no further recognition (such as authorship) is necessary. We disagree with this position as well, and argue instead that if they meet the criteria for authorship, they should be offered authorship, regardless of whether they are paid.

The primary criterion for authorship is a substantial level of intellectual involvement in the work being reported. This intellectual involvement can come in several forms, often conceived in three primary areas: (1) conception and funding of the ideas; (2) execution of the research plan; and (3) analysis and writing of the final product. Today, it is generally agreed that significant contribution to even one of these three areas may justify inclusion as an author on the final paper. It is likewise generally agreed that field assistance or lab assistance alone typically does not meet the requirements for inclusion as an author, unless the assistant becomes intellectually involved in the logical decision-making linking the execution of the work to the objectives of the work. In other words, an assistant who notices that some procedure is not resulting in the information or data needed to proceed with the analysis, and who proposes a good solution to the procedural problem, is contributing intellectually to the execution phase to a significant level. This may sound somewhat murky, but in practice it is usually quite clear whether an assistant is proposing new ideas, new procedures, or solutions to problems, rather than continuing to repeat a flawed procedure.

Participants who contribute in other essential ways include those who approve and/or issue permits, those who process paperwork at multiple stages, those who plan logistical arrangements, and many other kinds of support activities. These persons deserve acknowledgment by name of person or institution, but do not deserve authorship unless they have contributed intellectually to the work as described. It is critical in healthy collaborations to have this explicit understanding, and to make sure that authorship and acknowledgment is given when deserved, regardless of other circumstances (e.g., whether an individual is paid or not).

12.1.7 Our example

In 2001, we initiated our first field season to explore issues of avian health in the Galapagos Islands. Personnel involved were numerous members of the veterinary staff at the Saint Louis Zoo, including staff veterinarians, veterinary residents, and veterinary technicians, beginning in the first year with Drs. Eric Miller and Mary Duncan, and the Zoo's head veterinary technician Jane Merkel, who later went on to receive her MS from UMSL for her work with this program. Their home institution, the Saint Louis Zoo, was and has remained committed to wildlife conservation in wild populations, not just within their walls. They have steadfastly supported their staff members' involvement in and contribution to field conservation efforts around the globe. They also committed to funding support for the collaboration that took the form for several years of an experienced wildlife veterinarian who committed to residing on the islands for one or more years (e.g., Drs. Tim Walsh, Nicole Gottdenker, Catherine Soos, and Sharon Deem). The other participating institution was the University of Missouri – St. Louis (UMSL), where one faculty member (PP) who had been conducting non-health-related research in Galapagos birds for several years, had recently taken the Des Lee Endowed Professorship in Zoological Studies linking UMSL with the Saint Louis Zoo. Following her arrival in St. Louis and formal association with the Saint Louis Zoo, the work on avian health emerged as a natural consequence of the sets of expertise available in the partner institutions. Numerous graduate students have participated in the program since the first 2001 field season, and between that time and this writing in 2017, 25 graduate degrees have been conferred based on research conducted in association with this program (16 MS degrees completed, 9 PhDs conferred, and two more nearing completion).

In addition to the two Saint Louis institutions, our in-situ local partners included the Galapagos National Park and the Charles Darwin Foundation, an international science advisory group that resides on the islands and manages the Charles Darwin Research Station. These four partners form the core group, and they have operated under a series of 5-year MOUs agreed upon and signed by all partner institutions. Under these agreements, the Galapagos National Park facilitates processing of permits (although annual permits are still necessary) for research and export of samples, and the Charles Darwin Foundation provides essential services such as arranging logistics of boat travel among islands, quarantine procedures for field teams, and provides accounting services for our work. This last piece is extremely helpful. We can estimate our in-country costs and wire the funds to the CDF office. Then, at the end of the season, they provide us with a detailed accounting of how the funds were spent, an essential service that we could not manage without. Since the inception of our program, we have invited a number of international experts to collaborate on particular projects or sub-projects; these include those with taxonomic expertise on particular groups of parasites (e.g., Dr. Hugh Jones for microfilarid nematodes, or Dr. Hans Klompen for mites and ticks), or expertise in particular analytical approaches such as modeling (e.g., Dr. Nakul Chitnis from the Swiss Tropical and Public Health Institute, or Dr. Robert Lacy from Brookfield Zoo). In general, these additional partners join us as authors on a paper or two to which they have contributed importantly, but do not join our multi-way multi-year MOU. Some short-term collaborations are more institutional than individual, such as our being permitted to use samples from the California Academy of Science's thousands of Galapagos collections to pinpoint the time of arrival of the poxvirus (Parker et al. 2011); even this institutional-level partnership relied on individual facilitation by CAS personnel like curator Dr. Jack Dumbacher to make this work possible. Other individuals have had more lasting involvement, such as Dr. Gediminas Valkiunas from the Nature Research Center in Vilnius, Lithuania, who has provided substantial guidance in our work on Haemosporidian parasites, when that group of parasites emerged as an important focus, and Dr. Hernan Vargas of the Peregrine Fund, who has contributed importantly to our field work, records and analyses on Galapagos penguins, Galapagos flightless cormorants, and Galapagos hawks. Just in 2016, we extended our formal partnership to add the ABG (Agencia de Bioseguridad Galapagos, an agency initiated in 2012 with the charge to understand the health threats to the domestic and wild animals of Galapagos) led by Dr. Marilyn Cruz, our longtime in-country veterinary collaborator, with whom we had worked on several coauthored papers before she took on the leadership of this important new agency. We now are further broadening our core group by adding the Institute for Zoology in London (Prof. Andrew Cunningham) and University of Leeds (Dr. Simon Goodman), both of whom have worked on related issues in Galapagos and with whom we have collaborated on several publications where our work overlaps (including this chapter). Those people who others might see as your biggest competitors should be your most important collaborators.

12.1.8 Costs and Benefits of Galapagos Collaborations

It is wonderful to conduct this kind of work in a place that has a local government commitment to the conservation of wildlife and restoration of natural systems when they have been disturbed. One example of this commitment is their multi-year program resulting in the eradication of feral ungulate populations that had established on several of the islands. Because of this massive effort, wild ungulate populations no longer exist on Espanola, Pinta, Santiago, and the northern (uninhabited) parts of Isabela (e.g., Campbell et al. 2004, Carrion et al. 2007, Cruz et al. 2009). We were able to sponsor two MS opportunities for young Ecuadorian scientists, Jose Luis Rivera and Mari Jaramillo (both involved in this volume), to measure the before-and-after impact of goat eradication on the population of Galapagos Hawks on the island of Santiago with collaborator Dr. Hernan Vargas of the Peregrine Fund (Rivera-Parra et al. 2012, Jaramillo et al. 2016). A second example is in progress now: Galapagos Verde, a gigantic undertaking to restore native plant communities on islands where they had been destroyed by the former presence of invasive ungulates or other human disturbances. Their efforts involve using innovative technologies to start plants at the CDF greenhouse and then transfer them to the field with enhanced chances of survival without requiring constant attention during the period of establishment. This program is led by Patricia Jaramillo of the CDF and strongly supported by the Galapagos National Park (Jaramillo et al. 2015).

In general, the Galapagos National Park is responsible for wildlife population monitoring and management throughout the archipelago. This is an enormous undertaking, as they are also responsible for the health and safety of human populations, and enforcement of regulations regarding safe and effective management of the Galapagos National Park and the plant, animals, and humans who live or travel within the Park. Since the entire archipelago is part of the Galapagos National Park and the waters surrounding the islands as the Galapagos Marine Reserve, it is not possible for them to be in all places at all times, and they must constantly be on alert for reports of poachers coming in from the edges of the Park and Reserve for illegal trafficking of such commodities as shark fins and teeth, sea cucumbers, and other items taken for their purported medicinal or culinary value. The Galapagos National Park maintains oceangoing vessels that patrol for these illegal activities, and with support from the Ecuadorian navy, attempts to detain and prosecute poachers. To this end, they have a legal staff for effective prosecution.

They also must oversee, approve, and follow the execution and results of all scientific work within the Park and Marine Reserve, which also requires a large staff. They have regularly provided rangers to accompany our teams when we need specific help with clearing trails (we do not cut vegetation ourselves) and occasionally with guidance across the trailless landscapes of the uninhabited islands. Finally, they are concerned about the safety of all tourists and scientists visiting Galapagos Islands, and stand ready to mount search and rescue missions in case of missing persons. Their responsibilities are multifaceted, complex, and enormous, and perhaps because of this enormity, the turnover rate in administrative levels is high.

Turnover of administrators at the Galapagos National Park complicates our work and makes the renewable MOUs important as a reminder to a new administration that an institutional commitment exists to their partners. There have been casualties to turnovers that lie outside of our MOU agreements. Part of our local capacity-building efforts include supporting the career progress of young scientists, bringing them occasionally to the US for accelerated training, and sending teams to Galapagos especially for local staff training (see Sect. 12.3, this chapter). These efforts may not give fruit to intended rewards when a new administration decides to put its efforts and resources elsewhere and not toward the promised job path of our trainees. There have been times when forward momentum on local capacity-building stalled and even reversed when a new Park administration decided that other issues were priorities and that international partners could take care of the disease work. Our position has always been that disease monitoring should be undertaken regularly, and that there should be a local agency or office with the resources in terms of funding, equipment, and skilled staff, to conduct routine tests without relying on international partners. This aspiration has yet to be fully realized, but we hope that the Agency for Biosecurity Galapagos (ABG) (see Chap. 10) will grow into this responsibility.

A further example of how the success and progress of initiatives can be dependent on relationships with the Park Administration comes from the Galapagos Genetics Epidemiology and Pathology Laboratory (GGEPL) project, which ran from 2004 to 2010, under a partnership involving the University of Leeds (UK), Zoological Society of London, Galapagos National Park Service, University of Guayaquil, and Concepto Azul (an Ecuadorian not-for-profit social enterprise). The project was primarily supported by the UK government's Darwin Initiative grant scheme, and aimed to establish a fully equipped laboratory, staffed by Ecuadorian personnel, which would give the Park Service the in-situ capability to investigate, manage, and set policy on wildlife health issues. The rationale was that wildlife disease often needs rapid diagnostics and interventions to minimize impact, and the Park would benefit from reducing its reliance on external expertise and support over time. The project trained several Ecuadorian personnel as veterinary pathologists, and laboratory technicians, while running its own research projects and collaborating with other international teams. As with the UMSL-St Louis Zoo projects, the governance of the GGEPL project by the partners was established via a MOU. A key aspiration of the project, and one of the criteria for funding, was that it should be sustainable by the local partners in the long term—and a commitment was made by the Park in the MOU to take on the running and responsibility of the GGEPL, once the UK government grant was completed. Unfortunately, despite the considerable investment into physical and human resources and a strong record of scientific and policy outputs, the Park chose not to fulfill its MOU commitment, and the laboratory closed in 2011 due to lack of funds. The reasons for this were complex, but contributing factors were undoubtedly the frequent changes in Park Director (8 during the course of the project), leading to a lack of institutional ownership of the project by the Park, and under the pressure of stretched resources and administrative capacity, a prevailing attitude that other international organizations would always step in to fill the gap. The overarching aim to enhance local capacity was thus stalled for a time, but many of the key Ecuadorian staff that were trained during the project (and the lab equipment) remained on the islands. In particular, Dr. Marilyn Cruz, who was GGEPL's lead veterinary pathologist, subsequently worked in other veterinary roles for the Park, before becoming director of ABG (and its predecessor SESA-SICGAL). Thus while the Park no longer has the direct capacity in wildlife health that was originally envisioned, some of that role is now filled by a new

Ecuadorian agency (ABG) that in part was helped to grow by the collaborative efforts of international and local teams. While GGEPL was operational, it followed the same principles of collaboration outlined for the UMSL-St. Louis Zoo programs, building teams of international and Ecuadorian scientists, Ecuadorian students and volunteers, with logistical and administrative support from the Galapagos National Park. The Park and other organizations were also represented on the GGEPL management committee and were consulted on research objectives needed to help them fulfill their own missions, such as managing health in the Galapagos tortoise captive breeding and repatriation program.

12.2 Host Government Regulations

12.2.1 Local Government Agencies and Their Regulations

In Chap. 10, we learned about the many agencies in Galapagos and their reporting relationships. Those most critical to our work have been the Galapagos National Park, the Charles Darwin Foundation, and since 2012 the Agency for Biosecurity Galapagos. Beginning in 2001, we sought permits directly from the Park, but arranged logistics on both inhabited and uninhabited islands through the Charles Darwin Foundation. Over time, the CDF took on a broader facilitation role, including submission of proposals for permits and oversight of reporting obligations. Since the origin of the Agency for Biosecurity Galapagos (ABG), which is an arm of the Ministry of the Environment of Ecuador, they have become our primary institutional partner, facilitating permits and housing. Our strong hope is that the ABG succeeds in its mission of monitoring, understanding, and protecting the health of all Galapagos animals, including domestic animals, livestock, and wildlife. Even as reporting relationships change over time, it is critical to have a primary partner agency that will guide your efforts to maintain compliance with local regulations.

The Galapagos National Park publishes a Field Guide for Research in Galapagos, in which they lay out all expectations for behavior on uninhabited islands, as well as expectations for behavior and procedures on inhabited islands. First, of overarching importance, is that researchers may only catch and handle individuals of species for which they have specific permits during the active period of those permits. And they may only capture and handle the number permitted of each species. For any individual bird caught accidentally but not on the list of permitted species, or for any individual of a permitted species beyond the number permitted, those individuals must be released immediately. Prior to camping on an uninhabited island, researchers must go through a 48-h quarantine process during which all of their camping materials (all scientific and camping gear and all clothing) must be thoroughly inspected by trained GNP and CDF personnel, then fumigated in a sealed room for 48 h. All food to be taken to the uninhabited island must be frozen for 48 h at the GNP, in order to kill any insects that might be in grain products, etc. Furthermore, the GNP specifies which brands of foods may be used, as some jams and jellies are prepared in ways that would allow escaped seeds to grow, while others are not. The GNP also requires that all refuse be removed from an uninhabited island on which researchers have camped. All garbage is removed in bags and disposed of on return to Santa Cruz, or burned prior to departing the island, as specified by current regulations (which also change over time). The camp site itself is sometimes specified by the GNP on particular islands, and it is never far from the shoreline, as equipment includes gas canisters for cooking and jerry-cans of fresh water for the entire team for the duration of their time on the island. A latrine area must be identified that is used as a common latrine area by the team, below the high tide line for effective removal of wastes. Each field team has a designated leader, often a senior graduate student or a Zoo veterinary staff member with extensive experience on the particular sub-project in familiarity with the location and Galapagos regulations. This leader is responsible for the team members and their behavior. All team members understand before joining the team that the leader has final decision-making authority on assignments to sub-teams each day. Ultimately, of course, if a problem arises on any field team, the person who is ultimately responsible is the person whose name is on the research permit from the Galapagos National Park. A preliminary report to the Park is required before leaving the islands, and a more detailed report is due within 6 months (the timeline of this requirement has changed over the years).

12.2.2 Our Own Field Protocols

We capture small birds by mist-netting, or with hand nets depending on the species, and our own netting protocols are possibly the most conservative that exist. We never put up more nets than the number of people on our netting team, and no net is ever left without an observer for any time. Birds are removed immediately upon capture, and put into holding bags, and if there are not enough people to both watch the net and process the captures, we close the nets until a person is available to watch. Holding bags containing birds are hung in the shade in chronological sequence so that processing is on a first-in first-out basis. No bird should be held more than 15 min in a bag before processing. If captures become so numerous that the 15-min limit is reached, birds must be released. However, we would typically shift people from nets to processing when there are that many birds backed up. Our aim is to harm not a single bird and to leave the island unsullied. We ardently do not want to be part of the problem we are studying.

Of course, we also have our own protocols for field processing of samples, and these can be exacting, particularly on an active capture day. Birds are handled by experienced trained handlers who record standard morphological measurements, and collect small blood samples by sterile venipuncture of the brachial (wing) vein. We take no more than 1% of the body weight (i.e., no more than 100 µl from a 10-g bird). The blood is placed immediately into pre-prepared tubes containing 0.5 ml of a lysis buffer preservative that protects blood indefinitely even under ambient conditions, provided that no more than 100 ul blood is put into each 0.5 ml of preservative and it is immediately shaken vigorously. We normally take two samples for each bird (for small birds, we would split a 100 ul sample between two tubes of preservative). A small drop is used to make two thin blood smears on clean glass microscope slides, which are dried immediately (with a battery-operated fan when high humidity requires this assistance for fast drying). Slides are fixed in 100% methanol within 1 h (usually sooner) and are stained with Geimsa within 1 month. Each tube of preserved blood and each slide is labeled immediately upon collection with four items of information: Date, Location (for islands with multiple sampling sites, precise location), Species, Individual. For some sub-projects, individuals are banded for individual identification on subsequent capture, and these unique band codes are recorded on each sample and in the field data book. For sub-projects where this is not important, we may clip the end of a tail feather to make it blunt rather than rounded to avoid resampling the same individual on the same trip in the event of recapture. The labeling work often requires a labeler for each handler at particularly busy sites, but labeling is essential for later data analysis. The obsession with proper labeling has meant that we can accurately track each sample through time, including the years that samples may spend in our laboratory. By having four items of information on each sample, and duplicate samples for both blood and smears for each individual, we can hope to catch any labeling errors during subsequent sample processing. For example, if one label item is illegible, there are the duplicate samples to compare against, as well as the field record itself. Should the identity, location, species, or date of any sample remain uncertain after these comparisons, that sample would not be used in analyses. It has happened that we have been sent samples by other researchers that, in our opinion, did not have adequate information on the three most essential items (species, location, date) and we returned the samples unprocessed.

12.2.3 Specific Government Regulations and the Challenges They Present

Two regulations are particularly challenging for our work. The first is that for many years, possibly since the Galapagos National Park was created in 1959, it has been illegal to export a live animal from the Galapagos Islands. This regulation explains why there are no Galapagos animals in zoological institution collections around the world, with the possible exception of Galapagos tortoises that were taken away prior to that law and are still alive. This presents challenges for our work because much could be gained from conducting experimental infections of Galapagos birds with Galapagos pathogens, allowing the progress of infections to be monitored, advancement of the pathogen through developmental stages, even mortality rates of different age groups of hosts. Such experiments could be performed using individuals of the most abundant species to minimize population impacts, yet facilities do not exist on the islands to conduct such trials. The best that can be done is to use mainland relatives of Galapagos birds and arthropod vectors with mainland relatives of Galapagos pathogens; this restriction has some advantages, as it compels us to collaborate with scientists who routinely conduct these experiments and have excellent facilities and protocols for carrying out the experiments.

The second regulation that is problematic is that to receive an export permit to remove samples from Galapagos and Ecuador, the permit-holder must sign a statement saying that s/he understands that the samples are not their property, and that any remaining material after analyses are complete must be returned to Ecuador. Around the world, maintenance of ownership by "host" governments is typical, and understandable. This makes sense when the samples include whole organisms (e.g., insects preserved in ethanol), but problems arise when the samples are blood or DNA samples. Our primary samples are bird blood samples, which we bring to the US in the form of preserved whole blood, frozen blood serum (and the cells from which the serum had been removed, in preservative), and thin blood smears on glass slides. Often no serum remains following our laboratory analyses, and so there is nothing to return. The thin blood smears can be returned. The most problematic are the blood samples from which we have extracted DNA (containing both the DNA from the bird host as well as any parasite DNA that was in the bird's blood). These DNA samples will be extremely valuable to future researchers; had such samples existed when we began our work in 2001, we would have been able to do a much better job of pinpointing exactly when particular pathogens arrived. However, for indefinite storage without degradation, they should be frozen (some would store them at −80 °C, but we routinely store samples not under current investigation at −20 °C). Thus, a facility must be identified that not only has the capacity to store our 20,000+ samples from Galapagos birds, but those of many other researchers as well. Such a "DNA Bank" would be of significant international value, not only to future disease ecologists, but to future evolutionary biologists, and the value of such samples will continue to grow as technology advances and improves our ability to extract information from DNA. At this moment, there is no such repository for Galapagos DNA samples, and we strongly recommend that Ecuador and the Galapagos National Park agree on the location of such a repository. This will require careful curation, as different research groups undoubtedly handle samples differently in terms of extraction protocols, labeling, etc., and these differences must be understood and accommodated. The reason we suggest finding a facility on the mainland is that the infrastructure on the islands is vulnerable to its location out in the ocean and electricity, and often any kind of communication, is subject to outages. A mainland facility, possibly at a university that may already house and curate collections, would likely be more stable and appropriate.

12.3 Local Capacity-Building

12.3.1 International Variation in Specific Training

For effective conservation in any location on earth, the local people should not only be involved in the work, they should be involved at an "ownership" level; otherwise, it is a program managed from the "outside." If the local agencies and populations do not have conservation as a priority in their own value system, efforts by international groups will be difficult. This difficulty stems partly from the physical absence of the international groups for much of the year, but also because of their lack of personal identity with the landscape and its plants and animals. Local people must be involved and must "own" the problem and implement the long-term solutions. As was seen with the GGEPL, in the long term, a project's success and sustainability will always depend on the support of the local people and government. External funding for even the most successful of research projects will generally be for defined duration, driven by grant cycles. The capacity of international researchers or research groups to contribute may sometimes only last for the life of the research grant if the local people are not supportive and committed to making projects sustainable. Galapagos may be unique in the world in its identity as a natural wonder because of the endemic wildlife, and the natural state of many of the islands and their wild inhabitants. This preservation (and in many cases restoration) has been possible because of the commitment of the government of Ecuador, the Galapagos National Park, and their committed NGOs, such as the Charles Darwin Foundation, to practicing effective conservation based on the high value they place upon the wildlife of Galapagos. Because of this commitment, they have made enormous efforts to rid the islands of invasive exotics such as goats, donkeys, and pigs, and had the largest ever successes in those eradications (see Sect. 12.1.8). This involved working with international partners with extensive experience in such eradications, but then the effort was "owned" by local agencies until they succeeded.

What happens, though, when a new threat is perceived, one that cannot be seen with the naked eye? Where are the local experts who can help with detection and mitigation of arrival of a new pathogen that threatens their endemic wildlife? In the United States, schools of veterinary medicine are 4-year professional programs with competitive admission that requires an undergraduate degree, normally a Bachelor of Science degree with high grade point average and extensive volunteer or relevant experience in working with animals. Other countries may have programs in veterinary medicine, but they are often not post-baccalaureate programs like in the US, but instead are essentially extended undergraduate majors. In Peru, for example, veterinary training is a 5-year program, and three of the years focus on specific veterinary training, with the first two covering more general subjects. This is true in Ecuador as well. Because of this, it is difficult to find an Ecuadorian-trained veterinarian with knowledge that is as deep, as broad, or as current as one trained in the US or Europe. However, some programs outside of the US and Europe are highly regarded, including some in Brazil and Cuba.

12.3.2 Focal Training to Park and NGO Personnel, Identifying Key Individuals for Research Involvement

As early as 2001, we began offering training workshops in Galapagos to personnel from the Galapagos National Park and the Charles Darwin Foundation, as well as personnel from other local agencies. We had lectures on particularly important pathogens and how to recognize their symptoms, and purchased chickens from local farmers for hands-on training in taking blood samples and swab samples from birds. The participants responded with enthusiasm, and our classes were always filled. However, follow-up was challenging because no one, including Park personnel, was permitted to touch animals in the field that appeared sick, or even dead animals, which can be valuable sources of information. After 2 years of that kind of investment in training, we changed strategies and began focusing on particular individuals who were employees of local agencies who had the most appropriate prior training and sometimes had jobs that included responsibilities for animal health. These included Gustavo Jimenez at the Charles Darwin Foundation, and Marilyn Cruz, a well-trained veterinarian who has since emerged as a leader in Galapagos animal health.

We felt fortunate to meet Dr. Marilyn Cruz many years ago (see previous Sect. 12.1.8). A Galapagos native (she was born on the island of Floreana when its human population was fewer than 100 people), she left Ecuador to receive her DVM in Cuba, returning to Galapagos determined to help understand threats to the health of Galapagos animals. She served in a variety of capacities with the Galapagos National Park (and the GGEPL described in Sect. 12.1.8) and its short-lived internal focus on animal health, and worked with international researchers like us and others on a variety of projects. To date, Dr. Cruz has been involved in authorship on eight publications with our group on a variety of topics in Galapagos disease ecology. We were gratified when she was identified to direct the new Agencia for Biosecurity Galapagos (ABG), which is an arm of the Ministry of Environment of Ecuador and, we hope, less susceptible to the turnovers of the local Galapagos National Park leadership. The ABG was initiated in Galapagos in 2012. We met with Dr. Cruz again at an international workshop for animal health in Galapagos in 2015 and heard about her new position in the new agency, which is charged with understanding, monitoring, and mitigating disease threats to Galapagos animals, both farm animals on the four human-inhabited islands, and wildlife on all islands. This is an enormous charge. We told her at that meeting that we would help her in any way that was within our power.

12.3.3 Bringing Local Partner Personnel to International Sites for Training and Perspective-Building

Dr. Cruz reached out in spring of 2016, asking if we could help them establish testing protocols to run disease tests in their own laboratory facility, rather than having to send samples to the mainland, which could take much longer. This was the motivation for the GGEPL described in Sect. 12.1.8, where Dr. Cruz was employed as a veterinary pathologist. In the event of an outbreak, they felt the need to be able to respond quickly and accurately on their own. Since our expertise is with particular pathogens of particular wild animals, mostly birds, we solicited the collaboration of large animal veterinarians from the University of Missouri – Columbia College of Veterinary Medicine. With them, we sent a team in October 2016 to look at the ABG facilities, what equipment was on hand, and meet the ABG staff members. During that week, ABG staff took our team to visit farms, as well as the local slaughter facility on Santa Cruz. In March 2017, we invited them to visit our facilities. Five ABG staff members (two veterinarians and three lab technicians) arrived in St. Louis. None had been to the US before (except for one quick trip to Orlando by one), and none had seen snow, which fell on their first night. It was a nice sticky snow, so we made a quick snowman the first morning, then spent 1 week in St. Louis, split between the veterinary and pathology facility at the Saint Louis Zoo and the wildlife genetics and disease ecology laboratory at University of Missouri – St. Louis where we test samples from Galapagos (Fig. 12.1). All five of them saw the decisions that go into setting up a lab so that samples are properly stored and retrieved, and so that contamination can be avoided. They then spent a week at the Veterinary Diagnostic Lab at UM-Columbia Vet School, visited farms, received training in necropsy, and other aspects of veterinary training. On our third leg of training, an experienced senior graduate student from UMSL (Mari Jaramillo, an

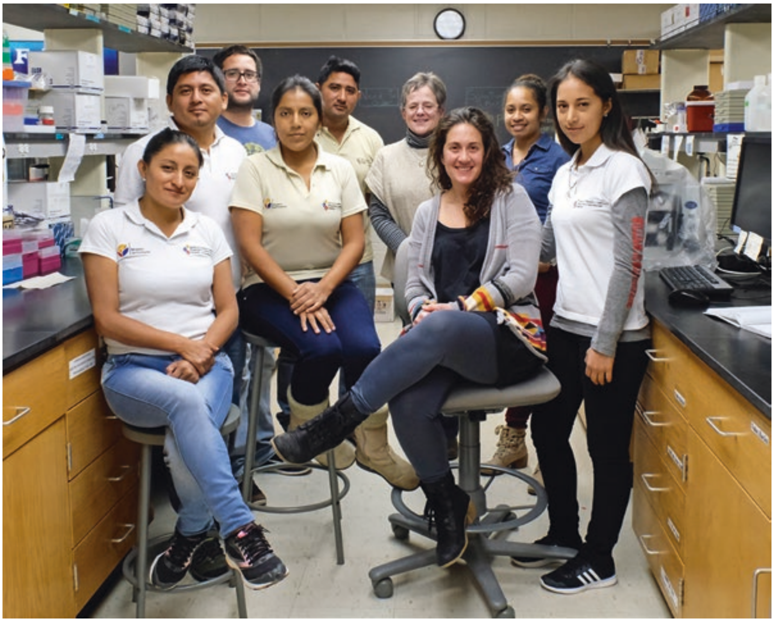

Fig. 12.1 In March 2017 five members of the ABC staff from Galapagos visited Missouri for 2 weeks intensive training in disease testing at the University of Missouri – St. Louis, the Saint Louis Zoo, and the University of Missouri College of Veterinary Medicine in Columbia

author in Chap. 6) visited the ABG facility in Puerto Ayora for 3 weeks to conduct on-site disease testing of the kind they learned at UMSL, but now in their own facility at ABG in Galapagos. We hope that this back-and-forth training will continue and expect other specific projects will emerge from this collaborative capacity building. We learned recently that the five individuals who visited us for training in early 2017 have won competitive permanent positions with ABG. These individuals are the future of animal health in Galapagos and even when they are at full capacity, we hope they will continue to involve us as needed.

12.4 Putting the Parts Together: How Collaboration Can Help Conservation

In 2008, new biosecurity regulations covering transport between the Ecuadorian mainland and the archipelago came into force, which were informed by the authors' research. The story of how research findings came to be translated into new practical conservation action provides an interesting case study on the importance of collaboration between scientists and local stakeholders. Although Galapagos encompasses a geographically small area, its governance is determined by a network of governmental agencies, with some accompanying inter-agency politics. This, combined with the complex political landscape of Ecuador and regular government changes in recent decades, potentially makes developing and enforcing new regulations a challenge without support from the right people. To be successful, such changes at the national level need to be driven by native agencies, even if the underpinning science is done in partnership with international researchers.

From the late 1990s a mosquito-borne viral disease called West Nile Virus (WNV) swept through the Americas after being introduced from a potential source in the Middle East or Europe (the exact origin is still debated). This is primarily an avian virus, though it can incidentally affect other vertebrate hosts including humans. WNV proved devastating for several taxonomic groups of birds in North America, driving large population declines, and by 2003 there was significant concern over the potential impact on Galapagos species should it be introduced to the archipelago. A workshop was organized in April 2004 by the GGEPL team, bringing together local agencies with leading experts on WNV and Galapagos avifauna, with the aim of evaluating the risk of different introduction pathways, impacts, and mitigation actions should WNV be introduced. The workshop concluded that WNV did pose a very significant risk, and that the most important introduction pathway would be via transport of infectious mosquitoes onboard aircraft flying to the islands from the mainland to service the needs of tourists and the local population. A peer-reviewed scientific paper based on the workshop outcomes was eventually published (Kilpatrick et al. 2006), but the workshop report and its recommendations were instrumental in convincing the local agencies that action was needed to reduce the WNV introduction risk.

Moving from the initial research findings to final implementation of new procedures was a long journey, taking more than 4 years, and was not something that could be accomplished by lone scientific research groups, or even individual local agencies, since none had the full set of expertise or necessary political authority. Once the local agencies (primarily the Galapagos National Park, SESA-SICGAL (the precursor biosecurity agency to ABG), and Ecuadorian Ministry of Environment) had decided action was necessary the process involved: (1) the Ministry of Environment drafting new biosecurity legislation (which required the introduction of mandatory insecticide treatment for aircraft flying to Galapagos, and restricting Galapagos flights to departures from Quito and Guayaquil only)—a process that was supported by personnel working for a United Nations GEF project on invasive species; (2) approval of the new legislation by the Ecuadorian government; (3) consultation with the Ecuadorian Civil Aviation Authority and airlines (TAME, Aerogal, LAN) about the new requirements and securing their cooperation; (4) defining what procedures should be used, identifying suppliers of chemicals and equipment, specifying training needs for personnel; costing everything and ensuring these were factored into ticket prices; (5) from September 2008, enacting the new measures and monitoring compliance and their effectiveness.

This pathway to implementation required communication and cooperation between at least three major Ecuadorian government agencies, a government ministry, two non-governmental organizations, and three commercial companies, plus the initial role of the scientists in describing the problem and identifying potential solutions (Fig. 12.2). The reasons this was accomplished successfully were due, first and foremost, to involving the main local stakeholders from the beginning—key personnel from the Galapagos National Park and SESA-SICGAL (the agency that preceded today's ABG) participated in the workshop and so were able to understand the importance of the issue and contribute ideas at an early stage, giving them ownership of the process. Second, the whole lobbying, consultation, and implementation process was facilitated by an individual with a combination of technical capacity and intimate local knowledge of each agency. In this case, the individual was Godfrey Merlen, a British expat resident in Galapagos since the 1970s, who works as an independent technical advisor to the National Park and other agencies. Godfrey has the advantage of being an eloquent lobbyist, a good communicator of the science, and connections with the top level of management in each agency—meaning that the urgency of the need to do something was impressed upon key decision makers, cementing their support. His position as an independent consultant, rather than an employee of a specific organization also meant that he was able to surf above inter-agency politics to get things done on relatively short timescales. This, combined with his driving passion for Galapagos conservation and skill at providing practical technical guidance to his Ecuadorian colleagues—such as helping the airlines to write the necessary procedures and source the fumigation chemicals from international suppliers, made everything work. Thus, the success of translating conservation research into conservation impact very much depends on effective communication between scientists, management agencies, and decision makers. Sometimes finding the right individual can be critical. Without Godfrey, the

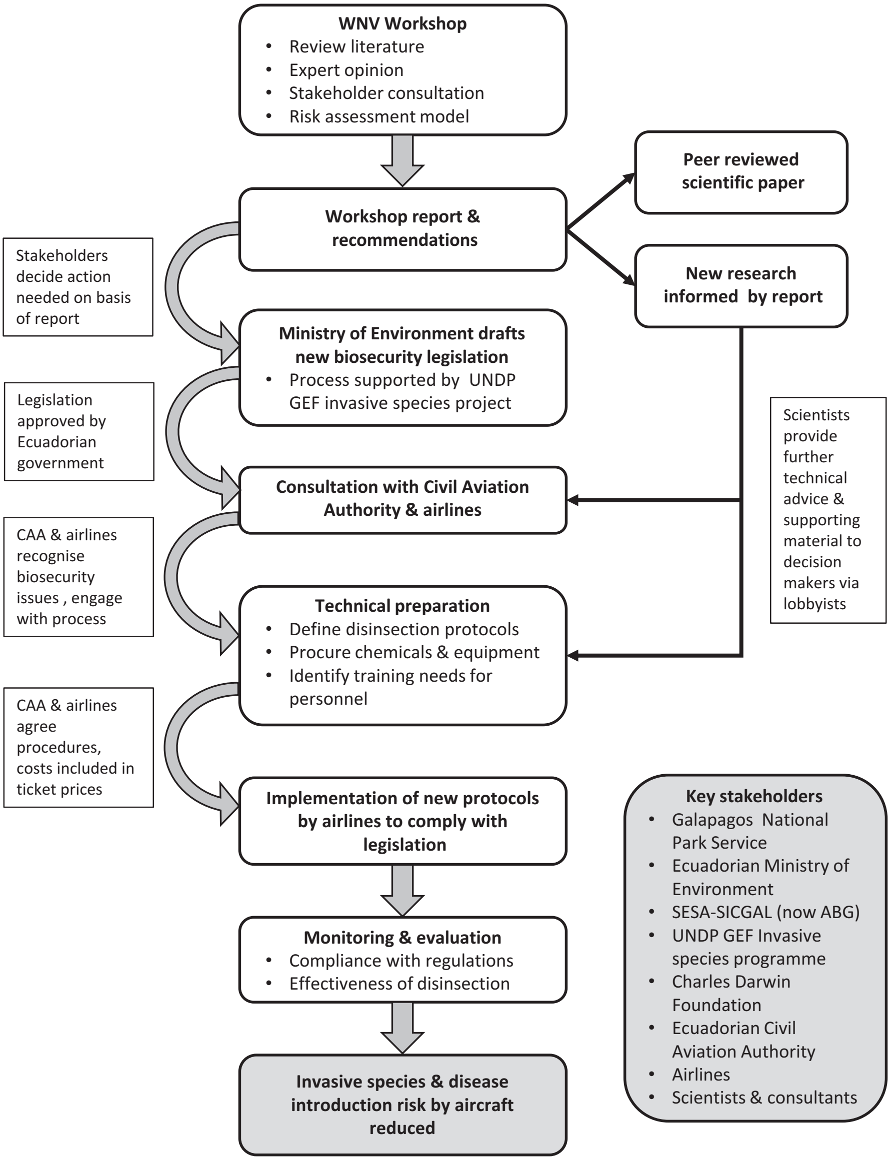

Fig. 12.2 Collaboration pathway for conservation change. This figure summarizes the pathway by which government agencies, scientists, and concerned individuals collaborated to result in new laws governing the routes by which airplanes may fly to Galapagos, and introduction of fumigation to reduce or eliminate arrival of insects to the islands on aircraft

new biosecurity measures may still have been implemented, but the process is likely to have been much slower and less efficient had researchers or an individual agency tried to act as the intermediary.

12.5 Closing Remarks

Throughout this experience, we have learned enormous amounts from our Galapagos collaborators. They know the place—it is their home. And the passion to protect the special wildlife and their understanding of the many reasons to protect the health of the farm animals is driving them to continue to improve their technical approaches to protect and conserve the islands and the wildlife residing there, and to ensure their safe inhabitation by humans. We could have done none of our work there without them, and our greatest hope is that they continue to call on us when they need our help; we expect that will be less and less over time, and eventually we will watch them from far away.

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