Chapter 1
Introduction and Overview

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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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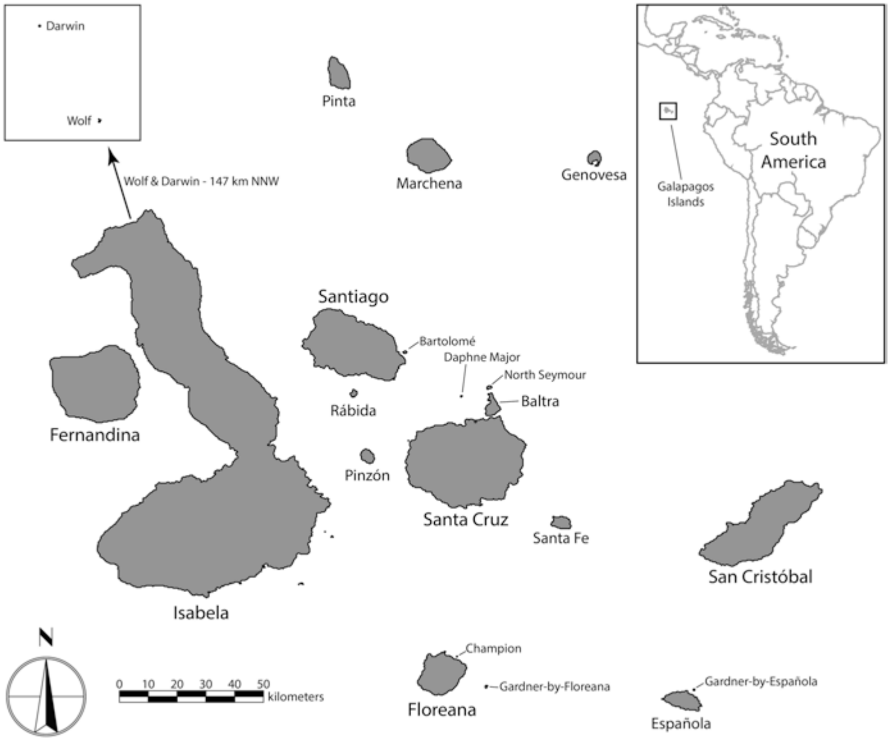

Fig. 1.1 Map of the Galapagos Islands. All of the islands labeled have been visited at least twice in our avian disease survey, including Darwin and Wolf. Some islands (e.g., Santiago, Santa Cruz, Isabela) are visited annually. Human populations occur on Santa Cruz, Isabela (far southern coast), San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