

Chapter 3
Colonization of Parasites and Vectors

Arnaud Bataille, Iris I. Levin, and Eloisa H.R. Sari

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
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 pres-
ence 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 impor-
tant factors are vector habitat preferences, host specificity, and dispersal capacity
(Ishtiaq et al. 2010). For this reason, the study of insular vector populations is criti-
cal 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 identi-
fied 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 para-
sites 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 intro-
duced 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 preva-
lenge and high densities on any given host. This happens because when hosts colo-
nize 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)* | Protozoa   | Swallow-tailed gull, Galapagos dove, Frigatebird spp., Nazca booby | Colonizing or migrating birds               |
| Und. Microfilaria*       | Nematode   | Flightless cormorant, Galapagos penguin                      | Colonizing or migrating birds               |
| Und. *Parahaemoproteus*  | Protozoa   | Blue-footed penguin                                          | Colonizing or migrating birds               |
| Und. *Plasmodium* spp. (3)| Protozoa   | Galapagos penguin                                            | Migrating birds                             |
| Und. *Trypanosoma* sp.*  | Protozoa   | Galapagos hawk                                               | Colonizing birds                            |
| **Directly-transmitted parasites and mites** | |                                                              |                                              |
| *Amerodectes atyaeoi*    | 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 marcazech*     | 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.* | 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*        | Protozoa   | Galapagos dove          | Colonizing birds       |
| *Isospora* spp. (6)*     | Protozoa   | Darwin’s finches.       | Colonizing birds       |
| *Isospora insularius*    | Protozoa   | Galapagos reptiles      | Colonizing reptiles    |
| *Mesalgoides geospizae*  | Mite       | Darwin’s finches        | Colonizing birds       |
| *Menacanthus distinctus* | Louse      | Galapagos flycatcher    | Colonizing birds       |
| *Myrsidea* spp. (3)*     | Louse      | Darwin’s finches, Galapagos mockingbirds. | Colonizing birds |
|                          |            | Yellow warbler          |                        |
| *Nycteridocaulus* sp.*   | 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* | Trematode  | Galapagos sea lion      | Colonizing or migrating mammals |
| *Philopterus insulicola* | Louse      | Galapagos vermilion flycatcher | Colonizing birds |
| *Physconelloides galapagensis* | Louse | Galapagos dove, Galapagos hawks | Colonizing or migrating birds |
| *Piagetiella* sp.        | Louse      | Brown pelican           | Colonizing or migrating birds |
| *Polysporella genovesae* | Protozoa   | Galapagos mockingbirds  | Colonizing birds       |

**Natural colonization (continued)**

**Directly-transmitted parasites and mites (continued)**

| Species                               | Type       | Known host in Galapagos | Likely mode of arrival |
|---------------------------------------|------------|-------------------------|------------------------|
| *Proctophyllodes darwinii*           | Mite       | Darwin’s finches        | Colonizing or migrating birds |
| *Renicola* sp.                       | Trematode  | Brown pelican           | Colonizing or migrating birds |
| *Ricinus marginatus*                 | Louse      | Galapagos flycatcher    | Colonizing birds       |
| *Strelkoviacarus* spp.*              | Mite       | Darwin’s finches        | Colonizing or migrating birds |
| *Trouessartia* spp. (2)*             | Mite       | Small ground finch, Galapagos flycatcher | Colonizing birds |
| *Tyranidectes berlai*                | Mite       | Galapagos flycatcher    | Colonizing birds       |
| *Xolalges palmai*                    | Mite       | Darwin’s finches        | Colonizing or migrating birds |
| *Zonorchis meyeri*                   | Trematode  | Galapagos rail          | Colonizing birds       |

**Disease vectors**

| Species                       | Type                   | Known host in Galapagos | Likely mode of arrival |
|-------------------------------|------------------------|-------------------------|------------------------|
| *Aedes taeniorhynchus*        | Fly                    | Multiple reptiles, mammal, and avian species | Direct colonization |

(continued)
| Species             | Type     | Known host in Galapagos                                      | Likely mode of arrival                  |
|---------------------|----------|-------------------------------------------------------------|-----------------------------------------|
| Amblyomma spp. (2 + 3) | Tick     | Marine iguana, Galapagos tortoise, land iguana              | Colonizing reptiles                     |
| Icosta spp. (2)     | Fly      | Galapagos hawk, flightless cormorant                        | Colonizing or migrating birds           |
| Microlynchia galapagoensis¹ | Fly      | Galapagos dove, mockingbrid spp.                           | Colonizing birds                        |
| Olfersia spp. (3)   | Fly      | Frigatebirds, flightless cormorant                          | Colonizing or migrating birds           |
| Ornithodoros spp. (2 + 1) | Tick    | Marine iguana, Galapagos tortoise, land iguana              | Colonizing reptiles                     |
| Ornithoica vicina   | Fly      | Unknown                                                     | Colonizing or migrating birds           |
| Tabanus vittiger¹    | 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 Paramyxovirus 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)       | Virus           | Chicken                 | Introduced chicken     |
| *Gammarcoronavirus*            | 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.

*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 *Craspedorhynchus* 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-
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 phylogenetic 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* origi-
nated 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 aenesens*, 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

![Hippoboscid fly on a Nazca booby (*Sula granti*; photo: Iris I. Levin)](image)
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
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.
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.
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.

![Eggs of the introduced southern house mosquito (*Culex quinquefasciatus*) deposited in an abandoned plastic container filled with water (Photos: Arnaud Bataille)](image)
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 hemoplasmodians, 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 hemoparasitic 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 hemoparasidian
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.

References

Alexander DJ, Aldous EW, Fuller CM (2012) The long view: a selective review of 40 years of Newcastle disease research. Avian Pathol 41:329–335
Amaral FR, Sheldon FH, Gamauf A, Haring E, Riesing M, Silveira LF, Wajntal A (2009) Patterns and processes of diversification in a widespread and ecologically diverse avian group, the bute- online hawks (Aves, Accipitridae). Mol Phylogenet Evol 53:703–715
Anderson JD, Fortner S (1988) Waved albatross egg neglect and associated mosquito ectoparasitism. Condor 90:727–729
Bar-David S, Lloyd-Smith JO, Getz WM (2006) Dynamics and management of infectious disease in colonizing populations. Ecology 87:1215–1224
Bataille A, Cunningham AA, Cedeno V, Patiño L, Constantinou A, Kramer LD, Goodman SJ (2009b) Natural colonization and adaptation of a mosquito species in Galapagos and its implications for disease threats to endemic wildlife. Proc Natl Acad Sci U S A 106:10230–10235
Bataille A, Cunningham AA, Cedeño V, Cruz M, Eastwood G, Fonseca DM, Causton CE, Azuero R, Loayza J, Martinez JD, Goodman SJ (2009a) Evidence for regular ongoing introductions of mosquito disease vectors into the Galapagos Islands. Proc Biol Sci 276:3769–3775
Bataille A, Cunningham AA, Cruz M, Cedeño V, Goodman SJ (2010) Seasonal effects and fine-scale population dynamics of Aedes taeniorhynchus, a major disease vector in the Galapagos Islands. Mol Ecol 19:4491–4504
Bataille A, Cunningham AA, Cruz M, Cedeño V, Goodman SJ (2011) Adaptation, isolation by distance and human-mediated transport determine patterns of gene flow among populations of the disease vector Aedes taeniorhynchus in the Galapagos Islands. Infect Genet Evol 11:1996–2003

Fig. 3.7 Screening domestic and migrating ducks for diseases threats to Galapagos fauna such as avian influenza (Photos: Arnaud Bataille)
Bataille A, Fournié G, Cruz M, Cedeño V, Parker PG, Cunningham AA, Goodman SJ (2012) Host selection and parasite infection in Aedes taeniorhynchus, endemic disease vector in the Galápagos Islands. Infect Genet Evol 12:1831–1841

Beadell JS, Gering E, Austin J, Dumbacher JP, Peirce MA, Pratt TK, Atkinson CT, Fleischer RC (2004) Prevalence and differential host-specificity of two avian blood parasite genera in the Australo-Papuan region. Mol Ecol 13:3829–3844

Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. Biol Lett 12:20150623

Bello FJ, Herrera GA, Sandoval JC, Escovar JE, Ruiz-Garcia M, Corena MD (2005) Colonization of Ochlerotatus taeniorhynchus from Riohacha, Colombia. J Am Mosq Control Assoc 21:28–32

Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004) Avian extinction and mammalian introductions on oceanic islands. Science 305:1955–1958

Bollmer JL, Kimball RT, Whitman NK, Sarosola JH, Parker PG (2006) Phyleogeography of the Galápagos hawk (Buteo galapagoensis): a recent arrival to the Galápagos Islands. Mol Phylogenet Evol 39:237–247

Brock PM, Hall AJ, Goodman SJ, Cruz M, Acevedo-Whitehouse K (2013) Immune activity, body condition and human-associated environmental impacts in a wild marine mammal. PLoS One 8:e67132

Brown CR, Brown MB (2004) Empirical measurement of parasite transmission between groups in a colonial bird. Ecology 85:1619–1626

Brown JKM, Hovmöller MS (2002) Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. Science 297:537–541

Bulgarella M, Quiroga MA, Brito vera GA, Dregni JS, Cunninghame F, Mosquera Munoz DA, Monje LD, Causton CE, Heimpel GE (2015) Philornis downsi (Diptera: Muscidae), an avian nest parasite invasive to the Galapagos Islands, in mainland Ecuador. Ann Entomol Soc Am 108:242–250

Bunbury N, Jones CG, Greenwood AG, Bell DJ (2008) Epidemiology and conservation implications of Trichomonas gallinae infection in the endangered Mauritian pink pigeon. Biol Conserv 141:153–161

Carpenter S, Wilson A, Mellor PS (2009) Culicoides and the emergence of bluetongue virus in northern Europe. Trends Microbiol 17:172–178

Castelletto ML, Gang SS, Okubo RP, Tselikova AA, Nolan TJ, Platzter EG, Lok JB, Hallem EA (2014) Diverse host-seeking behaviors of skin-penetrating nematodes. PLoS Pathog 10:e1004305

Causton CE, Peck SB, Sinclair BJ, Roque-Albelo L, Hodgson CJ, Landry B (2006) Alien insects: threats and implications for conservation of Galápagos Islands. Ann Ent Soc Am 99:121–143

Clark TM, Flis BJ, Remold SK (2004) Differences in the effects of salinity on larval growth and developmental programs of a freshwater and a euryhaline mosquito species (Insecta: Diptera, Culicidae). J Exp Biol 207:2289–2295

Clark NJ, Clegg SM (2015) The influence of vagrant hosts and weather patterns on the colonization and persistence of blood parasites in an island bird. J Biogeogr 42:641–651

Conrad PA, Miller MA, Kreuder C, James ER, Mazet J, Dabritz H, Jessup DA, Gulland F, Grigg ME (2005) Transmission of Toxoplasma: clues from the study of sea otters as sentinels of Toxoplasma gondii flow into the marine environment. Int J Parasitol 35:1155–1168

Cruz Martinez JD, Causton CE (2007) Análisis del riesgo asociado a las operaciones y rutas aéreas al Archipiélago de Galápagos. Charles Darwin Fundation, Puerto Ayora, Galápagos Islands, Ecuador. Available at http://www.feigalapagos.org/biblioteca.html

Curry RL, Grant PR (1989) Demography of the cooperatively breeding Galapagos mockingbird, Nesomimus parvulus, in a climatically variable environment. J Anim Ecol 58:441–463

Daszak P, Cunningham AA, Hyatt AD (2000) Emerging infectious diseases of wildlife–threats to biodiversity and human health. Science 287:443–449

Daszak P, Cunningham AA, Hyatt AD (2001) Anthropogenic environmental change and the emergence of infectious diseases in wildlife. Acta Trop 78:103–116
Dearborn DC, Anders AD, Schreiber EA, Adams RM, Mueller UG (2003) Inter-island movements and population differentiation in a pelagic seabird. Mol Ecol 12:2835–2843

Deem SL, Merkel J, Ballweber L, Vargas FH, Cruz MB, Parker PG (2010) Exposure to Toxoplasma gondii in Galapagos penguins (Spheniscus mendiculus) and flightless cormorants (Phalacrocorax harrisii) in the Galapagos Islands, Ecuador. J Wildl Dis 46:1005–1011

Deem S, Jiménez-Uzcátegui G, Ziemmek F (2011) CDF checklist of Galapagos zoopathogens and Parasites-FCD lista de especies de zoopatógenos y parásitos de Galápagos. In: Ruiz D, Guézou A, Ziemmek F (eds) Charles Darwin Foundation Galapagos species checklist–lista de especies de Galápagos de la Fundación Charles Darwin. Charles Darwin Foundation/Fundación Charles Darwin, Puerto Ayora, Galapagos. http://www.darwinfoundation.org/datazone/checklists/pathogens-and-parasites. Last updated 16 Jun 2011

Deem SL, Cruz MB, Higashiguchi JM, Parker PG (2012) Diseases of poultry and endemic birds in Galapagos: implications for the reintroduction of native species. Anim Conserv 15:73–82

Denkinger J, Gordillo L, Montero-Serra I, Murillo JC, Guevara N, Hirschfeld M, Fietz K, Rubianes F, Dan M (2015) Urban life of Galapagos sea lions (Zalophus wollebaeki) on San Cristóbal Island, Ecuador: colony trends and threats. J Sea Res 11:453–470

Diamond JM, Veitch CR (1981) Extinctions and introductions in the New Zealand avifauna: cause and effect? Science 211:499–501

Diaz NM, Mendez GS, Grijalva CJ, Walden HS, Cruz M, Aragon E, Hernandez JA (2016) Dog overpopulation and burden of exposure to canine distemper virus and other pathogens on Santa Cruz Island, Galapagos. Prev Vet Med 123:128–137

Dietrich M, Gomez-Diaz E, McCoy KD (2011) Worldwide distribution and diversity of seabird ticks: implications for the ecology and epidemiology of tick-borne pathogens. Vector Borne Zoonotic Dis 11:453–470

Dowler RC, Carroll DS, Edwards CW (2000) Rediscovery of rodents (genus Nesoryzomys) considered extinct in the Galápagos Islands. Oryx 34:109–118

Dubey JP (2002) A review of toxoplasmosis in wild birds. Vet Parasitol 106:121–153

Dunn JL, Wolke RE (1976) Dipetalonema spirocauda infection in the Atlantic harbor seal (Phoca vitulina concolor). J Wildl Dis 12:531–538

Eastwood G, Kramer LD, Goodman SJ, Cunningham AA (2011) West Nile virus vector competency of Culex quinquefasciatus mosquitoes in the Galapagos Islands. Am J Trop Med Hyg 85:426–433

Ewen JG, Bensch S, Blackburn TM, Bonneaud C, Brown R, Cassey P, Clarke RH, Pérez-Tris J (2012) Establishment of exotic parasites: the origins and characteristics of an avian malaria community in an isolated island avifauna. Ecol Lett 15:1112–1119

Fallon SM, Berringham E, Ricklefs RE (2005) Host specialization and geographic localization of avian malaria parasites: a regional analysis in the lesser Antilles. Am Nat 165:466–480

Farid HA, Hammad RE, Hassan MM, Morsy ZS, Kamal IH, Weil GJ, Ramzy RMR (2001) Detection of Wuchereria bancrofti in mosquitoes by the polymerase chain reaction: a potentially useful tool for large-scale control programmes. Trans R Soc Trop Med Hyg 95:29–32

Fenner F, Poole WE, Marshall ID, Dyce AL (1957) Studies in the epidemiology of infectious myxomatosis of rabbits: VI. The experimental introduction of the European strain of myxoma virus into Australian wild rabbit populations. J Hyg 55:192–206

Fessl B, Sinclair BJ, Kleindorfer S (2006) The life-cycle of Philornis downsi (Diptera: Muscidae) parasitizing Darwin’s finches and its impacts on nestling survival. Parasitology 133:739–747

Fonseca DM, Lapointe DA, Fleischer RC (2000) Bottlenecks and multiple introductions: population genetics of the vector of avian malaria in Hawaii. Mol Ecol 9:1803–1814

Fonseca DM, Smith JL, Wilkerson RC, Fleischer RC (2006) Pathways of expansion and multiple introductions illustrated by large genetic differentiation among worldwide populations of the southern house mosquito. Am J Trop Med Hyg 74:284–289

Font WF (2003) The global spread of parasites: what do Hawaiian streams tell us? Bioscience 53:1061–1067

Fournié G, Goodman SJ, Cruz M, Cedeño V, Vélez A, Patiño L, Millins C, Gibbons LM, Fox MT, Cunningham AA (2015) Biogeography of parasitic nematode communities in the Galápagos giant tortoise: implications for conservation management. PLoS One 10:e0135684
Frankham R (1997) Do island populations have less genetic variation than mainland populations? Heredity 78:311–327

French SS, DeNardo DF, Greives TJ, Strand CR, Demas GE (2010) Human disturbance alters endocrine and immune responses in the Galápagos marine iguana (Amblyrhynchus cristatus). Horm Behav 58:792–799

Godfrey SS, Nelson NJ, Bull CM (2011) Ecology and dynamics of the blood parasite, Hepatozoon tuatarae (Apicomplexa), in tuatara (Sphenodon punctatus) on Stephens Island, New Zealand. J Wildl Dis 47:126–139

Gottdenker NL, Walsh T, Jiménez-Uzcátegui G, Betancourt F, Cruz M, Soos C, Miller RE, Parker PG (2008) Causes of mortality of wild birds submitted to the Charles Darwin Research Station, Santa Cruz, Galápagos, Ecuador from 2002–2004. J Wildl Dis 44:1024–1031

Gottdenker NL, Walsh T, Vargas H, Merkel J, Jimenez R, Gustavo U, Miller RE, Dailey M, Parker PG (2005) Assessing the risks of introduced chickens and their pathogens to native birds in the Galápagos archipelago. Biol Conserv 126:429–439

Hailer F, Schreiber EA, Miller JM, Levin II, Parker PG, Chesser RT, Fleischer RC (2010) Long-term isolation of a highly mobile seabird on the Galápagos. Proc Biol Sci 278:817–825

Hall-Stoodley L, Stoodley P (2005) Biofilm formation and dispersal and the transmission of human pathogens. Trends Microbiol 13:7–10

Hardy DE (1960) Insects of Hawaii, Diptera, vol 10. University of Hawaii Press, Honolulu, HI

Hardy JL, Rosen L, Reeves WC, Scriveri RP, Presser SB (1984) Experimental transovarial transmission of St. Louis encephalitis virus by Culex and Aedes mosquitoes. Am J Trop Med Hyg 33:166–175

Hoberg EP, Brooks DR (2008) A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host–parasite systems. J Biogeogr 35:1533–1550

Howard LO (1889) Scientific results of explorations by the U.S. fish commission steamer “albatross”. No. V. Annotated catalogue of the insects collected in 1887–88. Proc US Natl Mus 12:185–216

Iqbal M, Austin AD (2002) New species of the Australian endemic wasp genus Notosigalphus van Achterberg and Austin (hymenoptera: Braconidae) from Flinders Island, Tasmania. Aust J Entomol 41:149–154

Ishtiaq F, Guillaumot L, Clegg M, Phillimore AB, Black RA, Owens IPF, Mundy NI, Sheldon BC (2008) Avian haematozoan parasites and their associations with mosquitoes across Southwest Pacific Islands. Mol Ecol 17:4545–4555

Ishtiaq F, Clegg SM, Phillimore AB, Black RA, Owens IPF, Sheldon BC (2010) Biogeographical patterns of blood parasite lineage diversity in avian hosts from southern Melanesian islands. J Biogeogr 37:120–132

Harris JD, Joao PMCM, Ana P (2011) Molecular characterization of Hepatozoon species in reptiles from the Seychelles. J Parasitol 97:106–110

Jones KE, Patel NG, Levy MA, Storeygard A, Balk D, Gittleman JL, Daszak P (2008) Global trends in emerging infectious diseases. Nature 451:990–993

Juliano SA, Lounibos PL (2005) Ecology of invasive mosquitoes: effects on resident species and on human health. Ecol Lett 8:558–574

Kay BH, Farrow RA (2000) Mosquito (Diptera: Culicidae) dispersal: implications for the epidemiology of Japanese and Murray valley encephalitis viruses in Australia. J Med Entomol 37:797–801

Keeling MJ, Woolhouse MEJ, Shaw DJ, Matthews L, Chase-Topping M, Haydon DT, Cornell SJ, Kappey J, Wilesmith J, Grenfell BT (2001) Dynamics of the 2001 UK foot and mouth epidemic: stochastic dispersal in a heterogeneous landscape. Science 294:813–817

Keesing F, Belden LK, Daszak P, Dobson A, Harvell CD, Holt RD, Hudson P, Jolles A, Jones KE, Mitchell CE, Myers SS, Bogich T, Ostfeld RS (2010) Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature 468:647–652

Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W (2009) A global assessment of endemism and species richness across island and mainland regions. Proc Natl Acad Sci U S A 106:9322–9327
Kilpatrick AM, Kramer LD, Campbell SR, Alleyne EO, Dobson AP, Daszak P (2005) West Nile virus risk assessment and the bridge vector paradigm. Emerging Infect Dis 11:425–429

Kilpatrick AM, Chmura AA, Gibbons DW, Fleischer RC, Marra PP, Daszak P (2006a) Predicting the global spread of H5N1 avian influenza. Proc Natl Acad Sci U S A 103:19368–19373

Kilpatrick AM, Daszak P, Goodman SJ, Roog H, Kramer LD, Cedeno V, Cunningham AA (2006b) Predicting pathogen introduction: West Nile virus spread in Galápagos. Conserv Biol 20:1224–1231

Klassen GT (1992) Coevolution: a history of the macroevolutionary approach to studying host–parasite associations. J Parasitol 78:573–587

Koop JAH, Huber SK, Laverty SM, Clayton DH (2011) Experimental demonstration of the fitness consequences of an introduced parasite of Darwin’s finches. PLoS One 6:e19706

Labarthe N, Guerrero J (2005) Epidemiology of heartworm: what is happening in South America and Mexico? Vet Parasitol 133:149–156

Labarthe N, Serrao ML, Melo YF, de Oliveira SJ, Lourenço-de-Oliveira R (1998) Potential vectors of Dirofilaria immitis (Leidy, 1856) in Itacoiatira, oceanic region of Niterói municipality, state of Rio de Janeiro, Brazil. Mem Inst Oswaldo Cruz 93:425–432

Lang JD (2003) Factors affecting immatures of (Diptera: Culicidae) in San Diego County, California. J Med Entomol 40(4):387–394

Levin II, Colborn RE, Kim D, Perlut NG, Renfrew RB, Parker PG (2016) Local parasite lineage sharing in temperate grassland birds provides clues about potential origins of Galapagos avian Plasmodium. Ecol Evol 6:716–726

Levin II, Parker PG (2014) Infection with Haemoproteus iwa affects vector movement in a hippoboscid fly-frigatebird system. Mol Ecol 23:947–953

Levin II, Outlaw DC, Vargas FH, Parker PG (2009) Plasmodium blood parasite found in endangered Galapagos penguins (Spheniscus mendiculus). Biol Conserv 142:3191–3195

Levin II, Valkiunas G, Iezhova TA, O’Brien SL, Parker PG (2012) Novel Haemoproteus species (Haemosporida: Haemoproteidae) from the swallow-tailed gull (Larriidae), with remarks on the host range of hippoboscid-transmitted avian Hemoproteids. J Parasitol 98:847–854

Levin II, Valkiunas G, Santiago-Alarcon D, Cruz LL, Iezhova TA, O’Brien SL, Hailer F, Dearborn D, Schreiber EA, Fleischer RC, Ricklefs RE, Parker PG (2011) Hippoboscid-transmitted Haemoproteus parasites (Haemosporida) infect Galapagos Pelecaniform birds: evidence from molecular and morphological studies, with a description of Haemoproteus iwa. Int J Parasitol 41:1019–1027

Levin II, Zwiers P, Deem SL, Geest EA, Higashiguchi JM, Iezhova TA, Jiménez-Uzcátegui G, Kim DH, Morton JP, Perlut NG, Renfrew RB, Suri EH, Valkiunas G, Parker PG (2013) Multiple lineages of avian malaria parasites (Plasmodium) in the Galapagos Islands and evidence for arrival via migratory birds: plasmodium in Galapagos birds. Conserv Biol 27:1366–1377

Levy JK, Crawford PC, Lappin MR, Dubovi EJ, Levy MG, Alleman R, Tucker SJ, Clifford EL (2008) Infectious diseases of dogs and cats on Isabela Island, Galapagos. J Vet Intern Med 22:60–65

Lindsay DS, Dubey JP (2009) Long-term survival of Toxoplasma gondii sporulated oocysts in seawater. J Parasitol 95:1019–1020

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20(5):223–228

Lounibos LP (2002) Invasions by insect vectors of human disease. Annu Rev Entomol 47:233–266

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ

MacLeod CJ, Paterson AM, Tompkins DM, Duncan RP (2010) Parasites lost–do invaders miss the boat or drown on arrival? Ecol Lett 13:516–527

Mangili A, Gendreau MA (2005) Transmission of infectious diseases during commercial air travel. Lancet 365:989–996

Masner L, Johnson N (2007) Xentor, a new endemic genus from Fiji (hymenoptera: Platygastroidea: Scelionidae) and description of three new species. Occas pap Bernice P. Bishop Mus 94:11–20
Rivera-Parra JL, Levin II, Parker PG (2014) Comparative ectoparasite loads of five seabird species in the Galapagos Islands. J Parasitol 100:569–577
Ruiz GM, Rawlings TK, Dobbs FC, Drake LA, Mullady T, Huq A, Colwell RR (2000) Global spread of microorganisms by ships. Nature 408:49–50
Santiago-Alarcon D, Outlaw DC, Ricklefs RE, Parker PG (2010) Phylogenetic relationships of haemosporidian parasites in new world Columbiformes, with emphasis on the endemic Galapagos dove. Int J Parasitol 40:463–470
Sardelis MR, Turell MJ, Dohm DJ, O’Guinn ML (2001) Vector competence of selected north American Culex and Coquillettidia mosquitoes for West Nile virus. Emerging Infect Dis 7:1018–1022
Sari EHR, Klompen H, Parker PG (2013) Tracking the origins of lice, haemosporidian parasites and feather mites of the Galápagos flycatcher (Myiarchus magnirostris). J Biogeogr 40:1082–1093
Sari HER, Parker PG (2012) Understanding the colonization history of the Galápagos flycatcher (Myiarchus Magnirostris). Mol Phylogenet Evol 63:244–254
Sato T, Higuchi T, Shibuya H, Ohba S, Nagami S, Shirai W, Watanabe H, Honda S (2002) Lingual squamous cell carcinoma in a california sea lion (zalophus californianus). J Zoo Wildl Med 33:367–370
Siers SR, Merkel J, Bataille A, Vargas FH, Parker PG (2010) Ecological correlates of microfilarial prevalence in endangered Galapagos birds. J Parasitol 96:259–272
Sinclair BJ (2017) Checklist of Galapagos Flies–FCD Lista de especies de Moscas y mosquitos de Galapagos. In: Bungartz F, Herrera H, Jaramillo P, Tirado G, Ruiz D, Guezo A, Ziemmeck F (eds) Charles Darwin foundation Galapagos species checklist–Lista de Especies de Galapagos de la Fundacion Charles Darwin. Charles Darwin Foundation/ Fundacion Charles Darwin, Puerto Ayora, Galapagos. http://darwinfoundation.org/datazone/checklists/terrestrial-invertebrates/diptera/ Last updated 12 May 2017
Smith KF, Carpenter SM (2006) Potential spread of introduced black rat (Rattus rattus) parasites to endemic deer mice (Peromyscus maniculatus) on the California Channel islands. Divers Distrib 12:742–748
Smith TG (1996) The genus Hepatozoon (Apicomplexa: Adeleina). J Parasitol 82:565–585
Soos C, Padilla L, Iglesias A, Gortdenker N, Don MC, Rios A, Parker PG (2008) Comparison of pathogens in broiler and backyard chickens on the Galapagos Islands: implications for transmission to wildlife. Auk 125:445–455
Strona G, Fattorini S (2014) A few good reasons why species-area relationships do not work for parasites. Biomed Res Int 2014:271680
Tatem AJ, Hay SI, Rogers DJ (2006a) Global traffic and disease vector dispersal. Proc Natl Acad Sci U S A 103:6242–6247
Tatem AJ, Rogers DJ, Hay SI (2006b) Global transport networks and infectious disease spread. Adv Parasitol 62:345–381
Telford SR Jr, Wozniak EJ, Butler JF (2001) Haemogregarine specificity in two communities of Florida snakes, with descriptions of six new species of Hepatozoon (Apicomplexa: Hepatozoidea) and a possible species of Haemogregarina (Apicomplexa: Haemogregarinidae). J Parasitol 87:890–905
Tenter AM, Heckerth AR, Weiss LM (2000) Toxoplasma gondii: from animals to humans. Int J Parasitol 30:1217–1258
Thiel T, Whiteman NK, Tirape A, Baquero M, Cedeno V, Walsh T, Jimenez Uzcátegui G, Parker PG (2005) Characterization of canarypox-like viruses infecting endemic birds in the Galápagos Islands. J Wildl Dis 41:342–353
Turell MJ, Beaman JR, Neely GW (1994) Experimental transmission of eastern equine encephalitis virus by strains of Aedes albopictus and Aedes taeniorhynchus (Diptera: Culicidae). J Med Entomol 31:287–290
Turell MJ, O’Guinn ML, Dohm DJ, Jones JW (2001) Vector competence of north American mosquitoes (Diptera: Culicidae) for West Nile virus. J Med Entomol 38:130–134
United Nations Educational, Scientific, and Cultural Organisation (UNESCO) (2006) Joint IUCN/UNESCO mission report: Galápagos Islands. United Nations Educational, Scientific and Cultural Organization, Paris
United Nations Educational, Scientific, and Cultural Organisation (UNESCO) (2010) State of conservation of world heritage properties inscribed on the list of world heritage in danger. United Nations Educational, Scientific, and Cultural Organisation, Paris

Valkiunas G (2005) Avian malaria parasites and other Haemosporidia. CRC Press, Boca Raton, FL
Valkiunas G, Santiago-Alarcon D, Levin II, Iezhova TA, Parker PG (2010) A new Haemoproteus species (Haemosporida: Haemoproteidae) from the endemic Galapagos dove, Zenaida galapagoensis, with remarks on the parasite distribution, vectors, and molecular diagnostics. J Parasitol 96:783–792

van Riper C, van Riper SG, Hansen WR (2002) Epizootiology and effect of avian pox on Hawaiian forest birds. Auk 119:929–942

van Riper C, van Riper SG, Lee Goff M, Laird M (1986) The epizootiology and ecological significance of malaria in Hawaiian land birds. Ecol Monogr 56:327–344

Warner RE (1968) The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. Condor 70:101–120

Weimerskirch H, Le Corre M, Maras F, Barbraud C, Tostain O, Chastel O (2006) Postbreeding movements of frigatebirds tracked with satellite telemetry. Condor 108:220–225

Wheeler E, Hong P-Y, Bedon LC, Mackie RI (2012) Carriage of antibiotic-resistant enteric bacteria varies among sites in Galapagos reptiles. J Wildl Dis 48:56–67

Whiteman NK, Dosanjh VS, Palma RL, Hull JM, Kimball RT, Sánchez P, Sarasola JH, Parker PG (2009) Molecular and morphological divergence in a pair of bird species and their ectoparasites. J Parasitol 95:1372–1382

Whiteman NK, Goodman SJ, Sinclair BJ, Walsh TIM, Cunningham AA, Kramer LD, Parker PG (2005) Establishment of the avian disease vector Culex quinquefasciatus say, 1823 (Diptera: Culicidae) on the Galápagos Islands, Ecuador. Ibis 147:844–847

Whiteman NK, Kimball RT, Parker PG (2007) Co-phylogeography and comparative population genetics of the threatened Galápagos hawk and three ectoparasite species: ecology shapes population histories within parasite communities. Mol Ecol 16:4759–4773

Whiteman NK, Parker PG (2005) Using parasites to infer host population history: a new rationale for parasite conservation. Anim Conserv 8:175–118

Whiteman NK, Sánchez P, Merkel J, Klompen H, Parker PG (2006) Cryptic host specificity of an avian skin mite (Epidermoptidae) vectored by louseflies (Hippoboscidae) associated with two endemic Galapagos bird species. J Parasitol 92:1218–1228

Wikelski M (1999) Influences of parasites and thermoregulation on grouping tendencies in marine iguanas. Behav Ecol 10:22–29

Wikelski M, Foufopoulos J, Vargas H, Snell H (2004) Galápagos birds and diseases: invasive pathogens as threats for island species. Ecol Soc 9(1) 5: http://www.ecologyandsociety.org/vol9/iss1/art5

Williams ES, Yuill T, Artois M, Fischer J, Haigh SA (2002) Emerging infectious diseases in wildlife. Rev Off Int Epizoot 21:139–157

Work TM, Massey JG, Rideout BA, Gardiner CH, Ledig DB, Kwok OCH, Dubey JP (2000) Fatal toxoplasmosis in free-ranging endangered ‘Alala from Hawaii. J Wildl Dis 36:205–212

Wyatt KB, Campos PF, Gilbert MTP, Kolokotronis S-O, Hynes WH, DeSalle R, Duszak P, MacPhee RDE, Greenwood AD (2008) Historical mammal extinction on Christmas Island (Indian ocean) correlates with introduced infectious disease. PLoS One 3:e3602

Ypma RJJ, Jonges M, Bataille A, Stegeman A, Koch G, van Boven M, Koopmans M, van Ballegooijen WM, Wallinga J (2013) Genetic data provide evidence for wind-mediated transmission of highly pathogenic avian influenza. J Infect Dis 207:730–735