Chapter 7
New Host-Parasite Relationships by Host-Switching

Diego Santiago-Alarcon and Jane Merkel

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

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

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7.1 Introduction

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

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

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

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

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

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

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

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

7.2 Case Studies

7.2.1 *The Galapagos Dove (Zenaida galapagoensis) and Haemoproteus parasites*

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

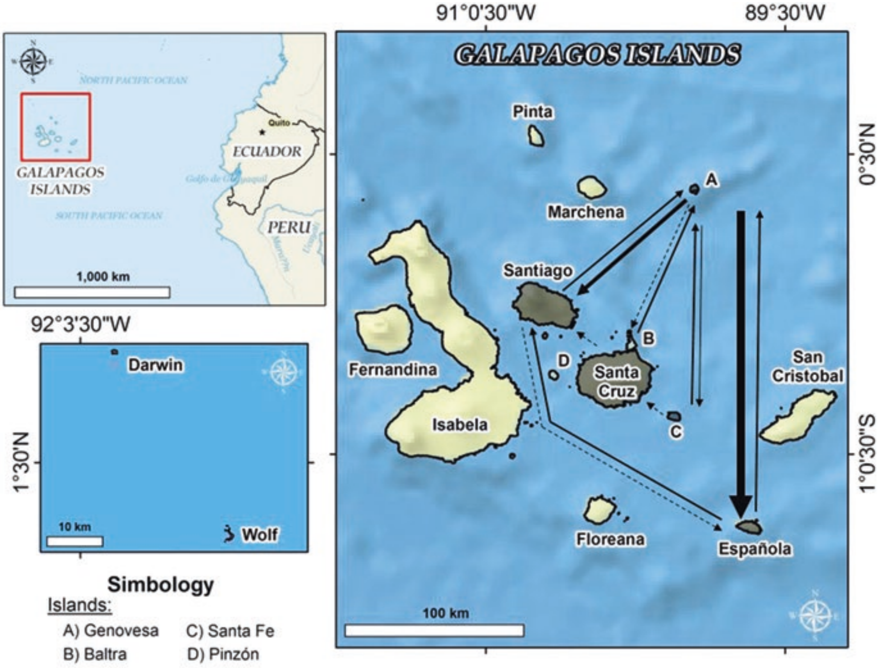

Fig. 7.2 Location of the Galápagos Archipelago and its different islands. Islands in *gray* color are those where Galápagos doves (*Zenaida galapagoensis*) were sampled. *Arrows* indicate microsatellite-estimated gene flow between islands; *arrow* width indicates the amount of directional gene flow

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

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

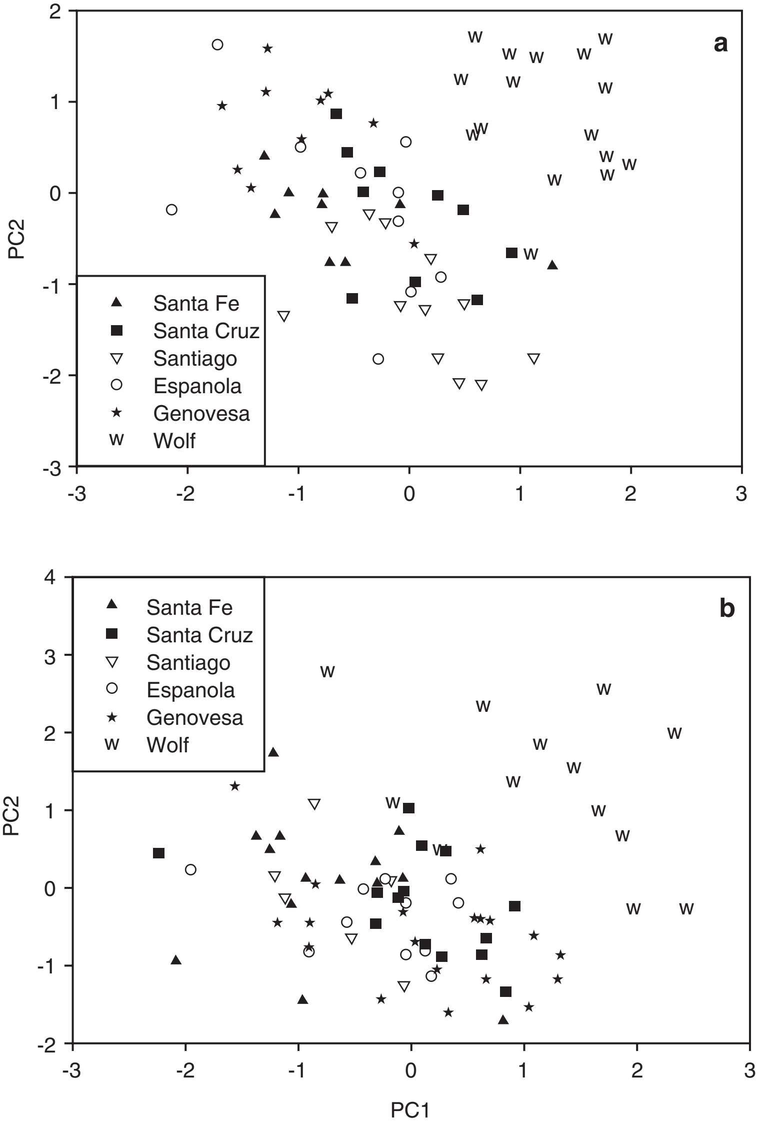

Fig. 7.3 (**a**) Morphological multidimensional space for female Galápagos doves captured on different islands across the archipelago. PC1 axis refers to overall body size and PC2 is an axis representing bill size and tarsus length. (**b**) Morphological multidimensional space for male Galápagos doves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

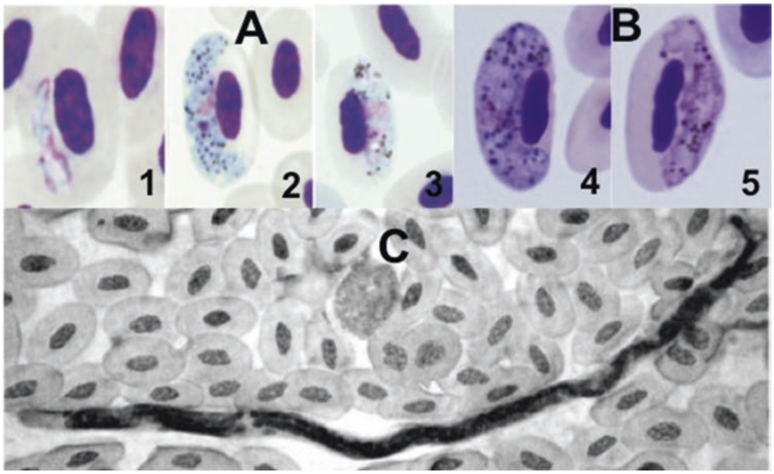

Fig. 7.4 (**a**) *Haemoproteus* (*Haemoproteus*) *multipigmentatus* (a parasite of pigeons and doves): (*1*) young developing gametocyte, (*2*) macrogametocyte, (*3*) microgametocyte. (Reproduced from Valkiunas et al. 2010) (**b**) *Haemoproteus* (*Haemoproteus*) *iwa* (a parasite of sea birds): (*4*)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

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

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

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

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

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

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

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

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

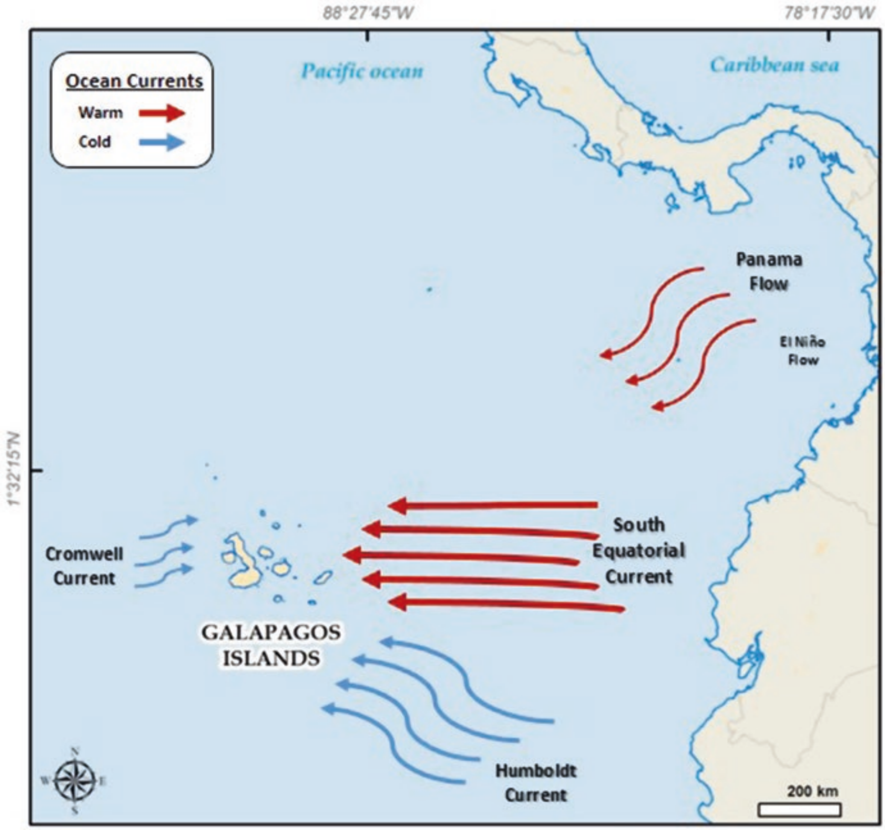

Fig. 7.5 Pacific oceanic currents bringing cold (Cromwell and Humboldt currents) and warm water (South Equatorial and Panama currents) to the Galápagos archipelago

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

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

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

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

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

[a] Proportion of distance from anterior end of microfilariae

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

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

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

7.3 Conclusion

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

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