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Conservation Medicine on the Galápagos Islands: Partnerships Among Behavioral, Population, and Veterinary Scientists

Patricia G. Parker, *University of Missouri–St. Louis*
Noah Kerness Whiteman, *University of Missouri*
R. Eric Miller, *University of Missouri*

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The fitness of animals in nature is mediated by behavior, through individuals' relative effectiveness in securing food, shelter, and mates. Especially in its ecological context, animal behavior is responsible for the movement of genes among population units and contributes strongly to the relative success and failure of particular lineages. Behavioral ecology, an evolutionary approach to the study of animal behavior that emerged as a discipline in the 1970s, has produced bodies of rigorous theory on reproductive and foraging strategies, social systems, and communication. These theories are increasingly being evaluated within a phylogenetic context.

During the same decades, developing population-genetics methods brought historical perspective with the phylogeographic approach, as well as current estimates of gene flow (even asymmetrical gene flow between population subunits), and accurate measures of individual reproductive success, each with resolution that was not possible through more traditional measures. These approaches mean that we can interpret the behavior of animals in a richer context than was possible before, accounting for the roles that individuals play in social systems, that social systems play in populations, and that populations play in relation to species. As we approached the problem of studying diseases among birds in the Galápagos Islands, we took the perspective of behavioral ecologists, curious about the variable roles among individuals, populations, and species in the dynamics of disease transmission.

Veterinary medicine, likewise, has evolved significantly in the decades since the 1970s, incorporating the latest developments from population biology, human medicine, and the biology and control of pathogenic organisms.

Seeking to understand threats of disease on the Galápagos Islands by joining these perspectives, we have embarked on studies that have implications in both basic and applied realms. At the outset, we anticipated that understanding the population dynamics of Galápagos birds would help us interpret parasite and pathogen distribution and host susceptibility, and that our clinical findings in parasite and pathogen distribution would inform our behavioral ecological studies of Galápagos bird populations.

Historically, the effect of disease on wildlife populations has been understudied, aside from a few cases of conservation interest. Parasiteinduced diseases have been underestimated, partly from the erroneous view that parasites that coevolve with their hosts do not have severe negative effects on them and partly from logistical difficulties (Gulland 1995). Disease, however, has been shown to affect survival, reproduction, and movement in host populations, and to affect community structure in turn (reviewed in Sco 1988). At the same time, emergent diseases are more common because of an expanding human population, associated growth of domestic animal populations, increased travel and commerce, human alteration of habitats, and global climate change (Daszak et al. 2000). Outbreaks of "mad cow disease" (bovine spongiform encephalopathy; Brown et al. 2001), foot-and-mouth disease (Picornaviridae: *Aphthovirus*; Kitching 1999), West Nile virus (*Flavivirus*; Lanciotti et al. 1999), SARS (*Coronavirus*), monkeypox (*Orthopoxvirus*), and avian influenza (Orthomyxoviridae) have demonstrated the virulence of some pathogens and their potential to cross over to new hosts, including humans. Thus, interest grows in the dynamics of infectious diseases in wildlife (Daszak et al. 2000, Friend et al. 2001), especially in threatened species, as we recognize the potential for disease to limit populations (Thorne and Williams 1988, Deem et al. 2001).

Parasites can have especially severe effects when they are transmitted to novel environments, where populations may lack natural resistance. Island populations may be at higher risk, because their parasite diversity is less than that of their continental counterparts (Lewis 1968a, b; Dobson 1988; Fromont et al. 2001; Goüy de Bellocq et al. 2002). Founders likely carry only a subset of the parasites found in the donor population, and virulent pathogens that need large host populations may be lost quickly (Dobson and May 1986, Dobson 1988). Paucity of parasites

reduces selection for resistance and enhances host population densities, both of which facilitate the transmission of introduced parasites (Dobson 1988).

The Galápagos Islands are volcanic in origin (Christie et al. 1992, White et al. 1993) and are located on the equator, ~1,000 km west of South America. Their isolation and relative desolation delayed their permanent colonization by humans until the 1800s, and their biodiversity remains mostly intact, only ~5% of species having been lost (Gibbs et al. 1999); 26 of 28 breeding landbird species are endemic, and there have been no extinctions of bird species. Currently, humans occupy only 4 of the 11 main islands, and most of those 4 islands and the remainder of the archipelago have been protected as the Galápagos National Park and Marine Reserve since the 1950s. However, the resident human population has grown rapidly and exotic species are continually being introduced despite increasing eff orts to exclude them. The Charles Darwin Foundation and the Galápagos National Park fear the introduction of avian diseases that could result in extinctions of Galápagos avifauna, similar to what happened in Hawaii (Warner 1968; van Riper et al. 1986, 2002; Wikelski et al. 2004). The appearance of avianpox-like lesions in domestic chickens (*Gallus gallus*) on the islands, and then in endemic birds, heightened concerns regarding the possibility of disease transmission from introduced birds to endemics. In fact, it was presumed that pox was brought to the archipelago via chickens in the 20th century (Grant et al. 2000). In the mid-1980s, the mosquito *Culex quinquefasciatus*, a vector of avian malaria, was reported from Galápagos, and its establishment has recently been confirmed (Whiteman et al. 2005). To date, however, the especially pathogenic strains of avian malaria of the genus *Plasmodium* have not been found. We have undertaken a large project, in collaboration with the Galápagos National Park and the Charles Darwin Foundation, to monitor disease status of Galápagos avian endemics and introduced birds. Partnering with international experts on major taxonomic groups of parasites, we use morphological and molecular approaches to identify organisms. We pursue phylogeographic studies to understand the history of the parasite lineages on the archipelago, and the relationships among parasite lineages and among parasites and host species. The result is a multilayered program examining the interplay between hosts and parasites and the behavioral ecology of both hosts and pathogens, which provides valuable information to the managers of this World Heritage Site and adds new dimensions to the study of evolutionary ecology of all Galápagos organisms, regardless of their body size.

Characterizing Parasites and Pathogens on the Galápagos Island

In 2001 and 2002, animal health professionals from the Saint Louis Zoo collaborated with biologists from the University of Missouri at St. Louis to offer Avian Health Workshops to personnel of the Charles Darwin Research Station, the Galápagos National Park, the customs and immigration office of Galápagos, and local veterinary professionals. Lectures covered the biology of avian pathogens and diagnostic symptoms of major avian diseases; hands-on workshops trained participants in phlebotomy for disease testing, smears for blood parasites, and necropsy protocol. Subjects were domestic chickens from local farms and Rock Pigeons (*Columba livia*) from extermination programs, on the human-inhabited islands of Santa Cruz and San Cristobal. In addition, we began the field surveys of natural populations of endemic birds. During the first two years, plasma and serum samples, blood smears, and cloacal swabs were sampled from Waved Albatrosses (*Phoebastria irrorata*), endemic to the island of Española (Padilla et al. 2003); Galápagos Hawks (*Buteo galapagoensis*) from eight islands; Galápagos Doves (*Zenaida galapagoensis*) from five islands (three uninhabited by humans and two inhabited; Padilla et al. 2004); and from Galápagos Penguins (*Spheniscus mendiculus*) and Galápagos Flightless Cormorants (*Phalacrocorax harrisi*) across their narrow ranges within the archipelago (Travis et al. 2006a, b). Sampling was later extended to other species

(see below). These endemic species were chosen because we were already involved in studies of their population biology and genetics. They represented two terrestrial species (one of which is the apex predator on the islands) and three marine species (one of which is pelagic and covers huge distances, the other two of which are flightless), and so could be seen as sentinel species for a large proportion of the ecological zones inhabited by birds in the Galápagos Islands. In addition, all are relatively largebodied, so sufficient samples could be taken to test for several pathogens. These ongoing population studies provided a background against which data on disease could be interpreted more fully. For example, our population-genetics studies show that the Galápagos Hawk is the most recent arrival of the endemic vertebrates on the archipelago (Bollmer et al. 2006), that since its arrival it has diversified rapidly among island populations, and that individuals very rarely move among islands (Bollmer et al. 2005). By contrast, the genes of Galápagos Doves move freely among the islands of the main archipelago (Santiago-Alarcón et al. 2006). Similar studies are underway for the penguins and cormorants. These data contribute to understanding the timing of arrival of hosts and their host-specific pathogens, their historical interisland movements, and the current dynamics of transmission of pathogens among islands and species. For example, comparison of hawks and doves suggests that the doves are far more likely to distribute pathogens among islands.

Veterinary and Evolutionary Approaches

Since 2002, the Saint Louis Zoo has funded a veterinary pathologist to reside on the islands as part of our research program. This person is present in the event of outbreaks and receives carcasses reported to the station, and is involved in a year-round training program for Ecuadorian veterinarians and veterinary pathologists on the islands. We broadened the field survey to include four seabird species on Genovesa and other island populations of landbirds. Upon capture, birds are handled briefly while morphological measures are made and ocular, choanal, and cloacal swabs are taken. Blood samples (≤1% body weight) are taken, and two smears are made on the spot. One drop of blood is preserved in lysis buffer for genetic analyses, whereas the remainder is spun in the field and plasma or serum frozen in liquid nitrogen. Later, samples and tissues are examined by serological tests, polymerase chain reaction (PCR), microscopy, and histopathology (on chickens and Rock Pigeons euthanized humanely as part of the extermination program, or on tissues from animals found dead) for complete blood counts, serum chemistry panel, and tests for enteric pathogens (*Salmonella, Shigella, Campylobacter* spp.), *Chlamydophila*, as well as for avian cholera, avian influenza, Newcastle disease, Paramyxovirus 2 and 3, West Nile Virus, infectious bronchitis, avian adenovirus, avian encephalomyelitis virus, avian reovirus, Marek's disease, and infectious bursal disease. Blood smears were examined for hemoparasites in all species, and positives were further examined by PCR for identification (Escalante et al. 1998, Ricklefs and Fallon 2002, Fallon et al. 2003). Introduced and endemic doves were tested for *Trichomonas gallinae*.

Ectoparasites are collected using a modified dust-ruffling technique (Walther and Clayton 1997; Whiteman and Parker 2004a, b) or, in the case of fresh carcasses, are removed directly from the hosts. Although dust-ruffling does not remove all ectoparasites (e.g., many mites), it is relatively noninvasive and allows a good estimation of ectoparasite infection intensity and prevalence (Walther and Clayton 1997). Ectoparasites are placed in 95–100% ethanol and stored at –20°C to ensure DNA preservation. DNA is extracted from exemplars from each host species or population, depending on the particular requirements of the study. A voucher method, in which an exoskeleton is retained as a voucher specimen, is used (Cruickshank et al. 2001, Whiteman et al. 2004). In the case of hippoboscid flies or other relatively large arthropods, a single leg is removed. DNA is extracted and used as a source of template DNA for PCRs. Arthropod-specific PCR primers are then used to amplify and sequence loci to be used in

population or phylogenetic studies (e.g., the 5' end of the cytochrome-*c* oxidase subunit I [COI] is used as a DNA barcode; Hebert et al. 2003). Thus, identifications of ectoparasites are made using a combination of morphological and molecular characters.

For many parasites and pathogens, DNA sequence data offer a larger set of characters than morphological data alone, for identification purposes. For example, with our collaborator, Kevin P. Johnson, we genotyped Galápagos Dove lice (*Columbicola macrourae* and Physconelloides galapagensis) that moved horizontally to Galápagos Hawks after the hawks fed upon the doves and showed that the dove lice were indeed derived from the local Galápagos Dove and were not a typical part of the hawk's ectoparasite community (Whiteman et al. 2004). Genotyping was necessary because female lice of these species are indistinguishable from some congeners. In the same study, we genotyped a louse nymph (Bovicola sp.) collected from a Galápagos Hawk that presumably moved from a goat carcass on which the hawks were feeding. In addition to providing additional characters for identification, DNA sequence data also allow estimation of relationships among Galápagoan taxa and their mainland relatives and estimation of gene flow of parasites among islands, a distinctly evolutionary approach that can build from and then inform the veterinary findings.

Endoparasites are identified using traditional taxonomy from blood smears and formalinpreserved specimens (when hosts are necropsied) and using PCR-based identification (Padilla et al. 2004). Moreover, microparasites (e.g., *Haemoproteus*, microfi lariae, *Trypanosoma*, avipoxvirus) obtained from avian blood, swabs, or biopsy are identified by extracting DNA (host and parasite) from host tissue samples (e.g., blood or skin biopsies) and PCRamplifying loci used to test for presence or absence (and then to calculate prevalence). Additionally, the amplicons from a subset of positive samples from each avian population are sequenced using standard techniques (e.g., cytochrome-*b* oxidase mitochondrial DNA [mtDNA] for haemoproteids; Fallon et al. 2003). Macroendoparasites are extracted using a method similar to the above when possible (preserving a part of the parasite as a voucher). All specimens are labeled fully and deposited in the appropriate institutions. Representatives of all lineages are deposited into the invertebrate collection at the Charles Darwin Research Station after all data have been collected (e.g., DNA sequencing, morphometrics, photographs).

Public databases, such as GenBank, have proved highly useful for obtaining outgroups for phylogenetic analyses, and we have relied on the use of the BLAST search option on the National Center for Biotechnology Information (NCBI) server to determine quickly and roughly the identities of the parasite lineages recovered within Galápagos taxa (e.g., trypanosomes, haemoproteids, avian skin mites, Phthiraptera). Eventually, our goal is to create a public database of all DNA sequences obtained from exemplars of all parasite taxa studied within the Galápagos Islands, with all available data on host, habitat, and collection information linked to the sequences, which will allow rapid determination of whether a given parasite has been recovered previously from a given host and locality. Thus, we can quantify the large amount of parasite diversity endemic to the Galápagos avifauna, which hopefully will encourage studies of other vertebrate groups that harbor their own unique parasite lineages (e.g., reptiles: Ayala and Hutchings 1974).

Preliminary Survey Results

Domestic and Introduced Birds

Domestic chickens were sampled on two of the four human-inhabited islands; several pathogens were detected by direct observation, including nematodes (*Dispharynx* sp. and *Capillaria* spp.) and the prozotoan *Toxoplasmosis gondii* (Go denker et al. 2005). Others were detected by antibody presence (not necessarily indicating active infection): avian adenovirus 1 (75%), infectious bronchitis CT (14%), infectious bronchitis MA (20%),

infectious bursal disease (23%), avian encephalomyelitis (46%), and Marek's disease (31%) (Go denker et al. 2005). Chickens interact closely with wild birds, and these parasites infect wild relatives of Galápagos endemics elsewhere (Dubey 2002, Forrester and Spalding 2003). Clearly, domestic chickens harbor pathogens, but the threat that these pose to the endemic avifauna is unclear. The population of introduced Rock Pigeons on the island of San Cristobal harbored *Trichomonas* (44%) in 2002 (Padilla et al. 2004). Chickens on Santa Cruz and San Cristobal habor fowlpox virus identical to that from chickens elsewhere (Thiel et al. 2005).

Endemics

We have sampled >3,100 birds from 17 native bird species from 13 islands (important fi ndings summarized in Table 1). The 17 species have been sampled in 36 island populations (see Table 1). Of these 36, 18 also have been sampled for ectoparasites. These 36 island populations, for which at least 20 individuals have been sampled, represent 22.5% of the 160 island populations of all seabirds and landbirds endemic at the species or subspecies level. Other endemics are represented by single specimens on which necropsy results are reported (e.g., Blue-footed Booby [*Sula nebouxii*] and Brown Pelican [Pelecanus occidentalis]). In most species, previously undescribed or new host records of previously known parasites were recovered (Table 1); in a few cases, results for particular focal species revealed no remarkable findings. For example, the single breeding population of Waved Albatross contained no remarkable findings, which allows us to characterize normal ranges for plasma chemistry, serology, and hematology (Padilla et al. 2003). In other cases, we were better able to characterize pathogens previously known to be present, such as *Avipoxvirus* (see below). Major pathogen findings are summarized briefly here in broad categories.

Blood Parasites

Nematodes.—In collaboration with Hernan Vargas, 448 Flightless Cormorants and 330 Galápagos Penguins were censused and sampled on four trips over two years throughout the ranges of both species. Prevalences of what appears to be the same nematode microfilarid (based on morphological evidence; H. I. Jones pers. comm.) were ~0.50 for Flightless Cormorant and lower, but still significant, for Galápagos Penguin (J. Merkel pers. comm.; Travis et al. 2006a, b). We are pursuing genetic studies of these nematodes. Preliminary sequence data from the COI locus, which has been shown to reliably diagnose nematode species (Blouin et al. 1998), revealed identical sequences between microfilarids obtained from blood samples of Galápagos Penguins and Flightless Cormorants, corroborating the morphological data. The results of a BLAST search of the sequences were conclusive. All the most similar sequences in GenBank to the two submitted were filarial nematode COI sequences, although the two Galápagosderived sequences were unique and differed from all others in GenBank by ~10% pairwise genetic distance. Nematodes of the genus *Contracecum* were also found in a Blue-footed Boobies, Brown Pelicans, and Yellow Warblers (*Dendroica petechia*) sampled opportunistically.

Apicomplexan blood parasites.— We observed *Haemoproteu*s in peripheral blood smears from three of four species of Genovesa Island seabirds (two endemic), as well as in the sympatric and endemic Galápagos Dove. Prevalences were 7 of 24 (29%) for Great Frigatebirds (*Fregata minor*), 2 of 23 (8.7%) for Redfooted Boobies (*Sula sula*), and 3 of 19 (15.8%) for Swallow-Tailed Gulls (*Larus furcatus*; Padilla et al. 2006). Almost all the 150 Galápagos Doves sampled on six islands had visible infections of a *Haemoproteus*-like parasite (Padilla et al. 2004); prevalence in Galápagos Doves was 11 of 26 (42%) on Genovesa. A small number of

Galápagos Penguins and Flightless Cormorants tested positive for apicomplexan blood parasites by PCR, though none has been positively identified on smears in either species. The genetic relationships among Apicomplexan blood parasites are under study, assessing whether there has been a radiation of blood parasites on these isolated islands.

Kinetoplast blood parasites.— We recovered a species of *Trypanosoma* of unknown identity in Galápagos Hawks of Santiago Island. We sequenced a small region of the small subunit ribosomal DNA (ssu rDNA) gene from bird-blood-derived DNA (Maslov et al. 1996), and a BLAST search on GenBank showed that this species is closely related to other raptorderived *Trypanosoma* species (J. Merkel and N. K. Whiteman pers. comm.). We do not know its distribution or prevalence.

Other endoparasites and poxviruses.— Opportunistic necropsies of seabirds revealed trematodes (*Renicola*), unidentified coccidians, and in Galápagos Doves on one island, antibodies of *Chlamydophila psittaci* (24% on Española, 6% overall; Padilla et al. 2004). *Chlamydophila psittaci* antibodies were also detected at high prevalence in Galápagos Penguin; lower prevalences of *C. psittaci* in the sympatric Galápagos Cormorant may have reflected the different testing methodologies used. *Chlamydophila* DNA was detected in several cormorants, but in no penguins (Travis et al. 2006a, b). Histopathology of cutaneous lesions from chickens, Yellow Warblers, and ground finches (*Geospiza* spp.) revealed inclusion bodies diagnostic of *Avipoxvirus* spp. Our characterization of the poxvirus in endemic passerine birds revealed two variants very closely related to canarypox virus, whereas domestic chickens on the islands are infected with the distinct fowlpox virus (Thiel et al. 2005). This suggests that the poxvirus did not "jump" from chickens to the endemic birds. Canarypox variants may also be endemic, perhaps arriving with avian colonists that gave rise to the endemic Galápagos avifauna, or transported by migrant passerines. Recombination analyses, however, indicated ancient recombination among all strains examined, which suggests that recombination could occur among sympatric *Avipoxvirus* strains in Galápagos Islands. Further phylogeographic studies of the virus in the endemic birds should clarify its closest relatives on the mainland.

Ectoparasites.— Four endemic bird species have been sampled for ectoparasites on 18 island populations (C in Table 1). We have recovered Acari of families Epidermoptidae and Argasidae, lice of genera *Pectinopygus, Piagetiella, Colpocephalum, Degeeriella, Craspedorhynchus, Columbicola, Physconelloides*, and hippoboscid flies (*Olfersia, Icosta*, and *Microlynchia*), as well as undescribed lice and unidentified mites (Table 1). These parasites vary markedly in life history and host specifi city in ways that we have investigated in our studies (see below). Opportunistic samples from other species have recovered unidentifi ed mites and lice of genera *Brueelia* and *Myrsidea*. Other researchers have reported ectoparasites from Galápagos birds as well (e.g., Palma 1995, Madden and Harmon 1998, Mironov and Perez 2002, Price et al. 2003, O'Connor et al. 2005). Extending this sampling eff ort to include all endemic bird taxa will recover many new species and contribute to our understanding of the relationships among parasite species as well as ecological relationships between parasites and their hosts.

Table 1. Endemic Galápagos birds sampled and parasites recovered. We have sampled 9 endemic seabird taxa and 25 endemic landbird taxa on 11 islands. This is not an exhaustive list of known parasites from these birds, but only those from our work. Many birds have not been sampled using dust-ruffling for ectoparasites (see text).

	Islands												
	Esp	Fer	Flo	Gen	Isa	Mar	Pta	SCI	SCz	SFe	Sgo	Ectoparasites	Endoparasites
Endemic seabirds													
Waved Albatross	B											**Acari**: *Ornithodoros* sp. (**Argasidae**)	
Flightless Cormorant		C			C							**Insecta**: *Pectinopygus* sp. (**Phthiraptera**); *Olfersia sordida* (**Hippoboscidae**). **Acari**: *Myialges caulotoon* (**Epidermoptidae**)	Und. microflilariae (**Nematoda**) *Chlamydophila psittaci*
Swallow-tailed Gull	A	A	A	B	A	A	A	A	A	A	A		Und. *Haemoproteus* sp. (**Haemoproteidae**)
Galápagos Penguin		C	C		C						C	**Insecta**: *Austrogoniodes demersus*. Note that this species has been reported from *Spheniscus demersus* (**Phthiraptera**) and may represent a cryptic species on *S. mendiculus*—see Banks et al. (2005).	Und. microflilariae (**Nematoda**); Und. *Haemoproteus* sp.; *Chlamydophila psittaci*
Endemic subspecies													
Blue-footed Booby			A		A			A		A	A		*Renicola* sp. (**Trematoda**); *Contracecum* sp. (**Nematoda**)
Magnificent Frigatebird				B	A			A					Und. *Haemoproteus* sp. (**Haemoproteidae**)
Brown Pelican	A	A	A		A				A		A	**Insecta**: *Piagetiella* sp. (**Phthiraptera**)	*Renicola* sp. (**Trematoda**); *Contracecum* sp. (**Nematoda**)
Landbirds: Endemic species													
Galápagos Hawk	C	C			C	C	C			C	C	**Insecta**: *Colpocephalum turbinatum*, *Degeeriella regalis*, Und. *Craspedorrhynchus* sp. (**Phthiraptera**); *Icosta nigra* (**Hippoboscidae**). **Acari**: *Myiagles caulotoon* (**Epidermoptidae**)	Und. *Trypanosoma* sp. (**Kinetoplastidae**)
Galápagos Dove	C	A	A	C	A	A	A	C	C	C	C	**Insecta**: *Columbicola macrourae*, *Physconelloides galapagensis* (**Phthiraptera**); *Microlynchia*	Und. *Haemoproteus* sp. (**Haemoproteidae**); *Chlamydophila psittaci*

Table 1. Continued.

	Islands												
	Esp	Fer	Flo	Gen	Isa	Mar	Pta	SCI	SCz	SFe	Sgo	Ectoparasites	Endoparasites
Galápagos Dove (*continued*)												*galapagensis* (**Hippoboscidae**). **Acari**: UnID feather mite (**Astigmata**)	(**Chlamydiaceae**)
Cactus Finch (*Geospiza scandens*)			A		A	A	A	A	B	A	A		Canarypox-like *Avipoxvirus*
Large Cactus Finch (*G. conirostris*)	A		A	B									
Large Ground Finch (*G. magnirostris*)		A		B	A				B		A		Canarypox-like *Avipoxvirus*
Medium Ground Finch (*G. fortis*)		A	A		A	A	A	A	B	A	A		Canarypox-like *Avipoxvirus*
Small Ground Finch (*G. fuliginosa*)	A	A	A		A	A	A	A	B	A	A		Canarypox-like *Avipoxvirus*; UnID coccidian
Vegetarian Finch (*Camarhynchus crassirostris*)		A	A		A			A	B		A	UnID mites (**Acari**)	Canarypox-like *Avipoxvirus*
Galápagos Mockingbird		B		B	A	B	B		B	B	A	**Insecta**: *Brueelia* sp., *Myrsidea* sp. (**Phthiraptera**)	Canarypox-like *Avipoxvirus*; UnID protozoan causing systemic infection; UnID coccidian
Hood Mockingbird	B											**Insecta**: *Brueelia* sp., *Myrsidea* sp. (**Phthiraptera**)	
Endemic subspecies													
Yellow Warbler	A	A	A	B	A	A	A	A	B	A	A		Canarypox-like *Avipoxvirus*; *Contracecum* sp. (**Nematoda**); UnID coccidian

Note: Only populations of endemic species or endemic subspecies are included. This selection comprises most of the land birds (except for domestic birds and occasional migrants). Parasites in bold are either known to be endemic to the archipelago or are likely endemic based on available information.

Abbreviations: A = breeding population; Und. = undescribed (new species); UnID: Unidentified (not identified beyond family or genus). B = breeding population for which we have sampled ≥20 individuals, taking blood samples, making blood smears, plasma or serum, and cloacal, choanal and conjunctival swabs. C =same as B, plus ectoparasite collections.

Islands: Esp = Española, Fer = Fernandina, Flo = Floreana, Gen = Genovesa, Isa = Isabela, Mar = Marchena, Pta = Pinta, SCI = San Cristobal, SCz = Santa Cruz, Sfe = Santa Fe, and Sgo = Santiago.

Effect of Parasites and Other Pathogens on the Endemic Birds

Pox-like symptoms have been described in several species and subspecies of endemic birds, including Galápagos Mockingbirds (*Nesomimus parvulus*), Galápagos Doves, Yellow Warblers, and some Galápagos finches (*Geospiza* spp., *Camarhynchus* spp.). Most data on the effects of avian pox are from mockingbirds (*Nesomimus* spp.). During the 1982–1983 El Niño event, 56% of Galápagos Mockingbirds displaying lesions died on Genovesa, compared with 39% of asymptomatic individuals (Curry and Grant 1989). During the same El Niño event on Isla Santa Cruz, 28% of juvenile Galápagos Mockingbirds exhibited apparent pox lesions; young birds without symptoms had higher resighting frequencies (72%) than those with lesions (0%), which suggested higher mortality for infected birds (Vargas 1987). Our work has barely begun to consider the health consequences of parasites and pathogens on their hosts. Hemoparasites in *Haemoproteus* have been traditionally considered incidental and relatively nonpathogenic parasites of birds and reptiles, though effects on host fitness have been demonstrated (Earlë et al. 1993, Merino et al. 2000, Marzal et al. 2005) and pathogenicity has been shown for certain hosts of certain hemoparasite species (Garvin et al. 2003). The pathogenicity of these parasites in the seabirds and doves sampled, or the effects on host fitness or reproductive success, are unknown. However, within Great Frigatebirds, birds infected with *Haemoproteus*-like parasites exhibited significantly higher heterophil-tolymphocyte concentration ratios than uninfected birds (Padilla et al. 2006). In chickens, this ratio increased when birds were exposed to social stress or corticosterone in feed, and it is thus considered to be an indication of environmental stress (Gross and Siegel 1983). In our studies, blood smears from each bird are used to identify circulating parasites and to conduct complete cell counts (i.e., heterophils, lymphocytes, monocytes, eosinophils, basophils), and estimate concentrations of overall leukocytes, each leukocyte type, and heterophil-tolymphocyte concentration ratios. Haptoglobin, an acute phase protein found in birds and other taxa (Delers et al. 1988), will be quantified using a serum assay available through Tri-Delta Diagnostics (Morris Plains, New Jersey) that we have used with success. Haptoglobin increases during inflammatory responses to trauma or infection. Blood chemistries will be quantified through commercial labs (Padilla et al. 2003, 2004, 2006; Travis et al. 2006a, b). We will compare these measures of response in infected and noninfected hosts within each species, and compare these differentials between "old" and "recent" parasites, as identified in our phylogeographic studies. For highprevalence parasites in particular populations, we will return to estimate resighting rates of hosts between years to estimate parasite-related mortality. Eventually, we and our colleagues would like to experimentally treat nesting nonthreatened birds (e.g., Great Frigatebirds) with antimalarial drugs to determine their ecological cost (e.g., Merino et al. 2000, Marzal et al. 2005). We are presently studying how removing lice from banded Galápagos Hawks affects the hawks' long-term survivorship.

Reflection on Behavioral Ecology

We will also use these results to estimate consequences of parasite infection for other components of fitness in the endemic avifauna of Galápagos. These studies will make connections back to our original interests in behavioral characteristics of island fauna. We will ask, for example, whether parasite infection affects the red coloration of the Red-footed Booby's (*S. Sula*) feet, and whether this, in turn, affects mating success (P. Baiao pers. comm.). We know that the high prevalence of adenovirus seropositivity in the Waved Albatross is not related to their pairing or reproductive success (K. P. Huyvaert pers. comm.), but we are aware that some of these disease organisms may have adverse fitness consequences for their hosts in a manner that is mediated through behavioral mechanisms such as pairing success or foraging efficiency, even when direct effects on morbidity are difficult to assess. For example, we have studied the ectoparasitic lice *Degeeriella regalis* and *Colpocephalum turbinatum* of the endemic Galápagos

Hawk. Number of lice per infected host correlates negatively with body condition and predicts territory status, such that nonterritorial birds carry higher parasite loads and are in poorer condition than territorial birds, even after controlling for age (Whiteman and Parker 2004a). New data suggest that newcomers to polyandrous Galápagos Hawk breeding groups on Santiago have significantly more lice than birds that have resided in the territories for at least one year, which is likely correlated with the newer birds' recent status as nonterritorial individuals (N. K. Whiteman et al. unpubl. data). In addition, the intensity of infection with the horizontally transmitted louse, *C. turbinatum,* varied positively with size of the infected Galápagos Hawk's social group, and intensity was significantly more similar within groups than between groups. This was not true for the vertically transmitted *D. regalis* (Whiteman and Parker 2004b). *Colpocephalum turbinatum* is the same louse that is useful for indicating relative immune function of different populations, because it encounters the immune system when it feeds on skin and growing feathers. We asked whether genetic diversity, parasite load, and immune function were related across all the breeding populations of the Galápagos Hawk, employing our quantitative sampling of *C. turbinatum*, estimates of island-population genetic diversity (Bollmer et al. 2005), and tests of natural constitutive antibodies (Matson et al. 2005) run on banked serum samples from the same individuals. We found that island populations of Galápagos Hawks with extremely little genetic diversity also have generally lower and less variable natural antibody titres and higher ectoparasite loads than larger, more genetically variable island populations (Whiteman et al. 2006). This reinforces the hypothesis that extinction risk of island endemics is attributable to mechanisms associated with reduced genetic diversity (Frankham 1996). Because of this finding, we recommended that the Galápagos National Park consider further restricting tourist visitation to the more isolated smaller islands, given that Galápagos Hawks on those islands are likely more susceptible to invasive diseases that may enter the archipelago.

Parasites that are not directly affected by host immune function reveal other aspects of the host–parasite interaction. *Degeeriella regalis* is a feather louse that occurs, within the islands, only on Galápagos Hawks. On the mainland, it occurs with regularity only on the Galápagos Hawk's putative sister species, the Swainson's Hawk (*B. swainsoni;* Riesing et al. 2003). This parasite is likely transmitted vertically between host individuals (Whiteman and Parker 2004a), transferring between parents and off spring during brooding. Comparative molecular data (N. K. Whiteman et al. unpubl. data) suggest that the parasite's mtDNA was diversifying more quickly than the host's under an island model of speciation (Hafner and Nadler 1990). We conservatively estimated that the Galápagos Hawk split from its common ancestor with the Swainson's Hawk <200,000 years BP and is, thus, the youngest known endemic bird lineage with the Galápagos Islands (Bollmer et al. 2006). The signature of a population bottleneck in the hawk lineage is seen at rapidly evolving nuclear minisatellite loci, which are nearly fixed within and different between island populations of the Galápagos Hawk (Bollmer et al. 2005) and in the mtDNA haplotype network, which shows very li le polymorphism, yet high structure (Bollmer et al. 2006). However, the parasite mtDNA network shows much more structure between and variability within island populations (N. K. Whiteman et al. unpubl. data). Because it is vertically transmitted and highly hostspecific, such parasites act as rapidly evolving "markers" that provide more insight into host history than we can get from the hosts themselves. The parasite network reveals aspects of host history (which haplotypes are derived from which ancestral haplotype), and we used this logic as a new rationale for parasite conservation (Whiteman and Parker 2005).

Surprisingly, our parasite surveys are among the first to examine parasite diversification within the Galápagos Islands, and the data gathered by our biotic inventory will be of use to scientists for decades. Our ongoing work will continue to uncover parasite lineages new to science. For example, there are no published reports of Phthiraptera from the following endemic birds, though each is a likely host to at least one species (Price et al. 2003): Lava Gull (*L.*

fuliginosus), Galápagos Rail (*Laterallus spilonotus*), eight species of Darwin's finches (*Geospiza* spp.), three mockingbird species (*Nesomimus* spp.), Galápagos Martin (*Progne modesta*), Galápagos subspecies of the Short-eared Owl (*Asio fl ammeus*), and others. Although two species of lice were reported previously from the Galápagos Hawk (de Vries 1973), our sampling (after receiving a tip from R. Palma) revealed that a previously undetected head louse, *Craspedorrhynchus* sp. (all in this genus are specific to raptors), which occurred in all island populations sampled, likely represents an endemic lineage. The detection of cryptic diversification within the Galápagos Islands, in addition to new species or new records, is certain. For example, an epidermoptid skin mite (a member of a family in which no DNA sequence data existed before our preliminary study), *Myialges caulotoon*, was previously reported from Flightless Cormorants and Galápagos Hawks, both Galápagos endemics (Madden and Harmon 1998). These mites have caused significant mortality in wild birds elsewhere, including an island endemic (Gilardi et al. 2001). Previously, however, only one specimen was collected from a Flightless Cormorant, and only morphological characters were used to identify these mites (Madden and Harmon 1998). Female mites of the genus *Myialges* are obligately vectored by hippoboscid flies or large chewing louse species (Fain 1965) and oviposit only on the insects. However, different species of flies infest Flightless Cormorants and Galápagos Hawks (Maa 1963, N. K. Whiteman et al. unpubl. data). Thus, we hypothesized that gene flow of the mites between avian hosts was limited given the hostspecificity of their fly vectors. We showed that individuals of *Myialges* from Flightless Cormorants and Galápagos Hawks differed significantly genetically even in areas where those two species co-occurred (e.g., Isla Fernandina). Our collaborator and expert on the Acari, H. Klompen, found consistent morphological differences between the series from each host, demonstrating the reciprocal illumination with morphological and molecular data to uncover new parasite lineages.

Disease epidemics have been implicated in the local and global extinctions of endangered species (van Riper et al. 1986, Thorne and Williams 1988, Laurance et al. 1996). Island populations may be particularly influenced by introduced pathogens because of their evolution in isolation, low levels of genetic heterogeneity, and increased population densities, all of which increase their susceptibility to new diseases and disease transmission among individuals. Also, island populations naturally tend to be small, making them more vulnerable to extinction. In addition, the parasites themselves are of extreme intrinsic value and interest. This partnership is describing the prevalence of parasites in terrestrial bird species and seabirds on the Galápagos Islands, assessing the history and origin of those parasite lineages, and beginning to assess the relative effects of recent and historical parasites on their hosts. In addition, we can use the empirical clinical data on health of individuals to inform our behavioral-ecology studies of mate choice, territory acquisition, reproductive success, and pa erns of movement. These results may contribute importantly to other conservation eff orts in other parts of the world. The results will also contribute a new dimension to the role that the Galápagos archipelago has served as evolution's laboratory by revealing the diversity of parasites that have evolved there, and are enabling us to begin quantifying the effects of both endemic and introduced parasites and pathogens.

On a final, personal note, it is clear to each participant in this program that the combined perspectives of population biology, behavioral ecology, and veterinary science have greatly enhanced the rigor and reach of our research, and have made each of us a better scientist. The authors of this paper include a behavioral– molecular ecologist (P.G.P.), an entomologist turned population biologist (N.K.W.), and a veterinarian and zoo administrator (R.E.M.). In coming to understand one another, we have each grown immeasurably, and we will forever see our work, however it develops, in a much broader way.

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