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Co-phylogeography and comparative population genetics of the threatened Galápagos hawk and three ectoparasite species: ecology shapes population histories within parasite communities

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Abstract

Comparative microevolutionary studies of multiple parasites occurring on a single host species can help shed light on the processes underlying parasite diversification. We compared the phylogeographical histories, population genetic structures and population divergence times of three co-distributed and phylogenetically independent ectoparasitic insect species, including an amblyceran and an ischnoceran louse (Insecta: Phthiraptera), a hippoboscid fly (Insecta: Diptera) and their endemic avian host in the Galápagos Islands. The Galápagos hawk (Aves: Falconiformes: *Buteo galapagoensis*) is a recently arrived endemic lineage in the Galápagos Islands and its island populations are diverging evolutionarily. Each parasite species differed in relative dispersal ability and distribution within the host populations, which allowed us to make predictions about their degree of population genetic structure and whether they tracked host gene flow and colonization history among islands. To control for DNA region in comparisons across these phylogenetically distant taxa, we sequenced ~1 kb of homologous mitochondrial DNA from samples collected from all island populations of the host. Remarkably, the host was invariant across mitochondrial regions that were comparatively variable in each of the parasite species, to degrees consistent with differences in their natural histories. Differences in these natural history traits were predictably correlated with the evolutionary trajectories of each parasite species, including rates of interisland gene flow and tracking of hosts by parasites. Congruence between the population structures of the ischnoceran louse and the host suggests that the ischnoceran may yield insight into the cryptic evolutionary history of its endangered host, potentially aiding in its conservation management.

Keywords: biogeography, co-evolution, comparative biology, life history, parasite diversification

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Introduction

Evolutionary biologists studying parasites have focused on macroevolutionary patterns and reconciling host and parasite phylogenies (Page 2003). However, the mechanisms of parasite diversification are less well known (Funk *et al*. 2000; Rannala & Michalakis 2003; Poulin 2006) and remain controversial (Huyse *et al*. 2005; Giraud 2006). Variation in natural history traits and geographical distributions are predicted to underpin parasite microevolution, co-evolutionary processes, and ultimately speciation, yet few studies exist at this scale (Price 1980; Nadler 1995; Criscione *et al*. 2005; Huyse *et al*. 2005).

Taxonomically and geographically limited studies are potentially useful for microevolutionary studies of parasites (Hafner *et al*. 2003). Specifically, comparative studies of multiple, co-occurring parasite species on a single host could be particularly illuminating (Nadler 1995). This

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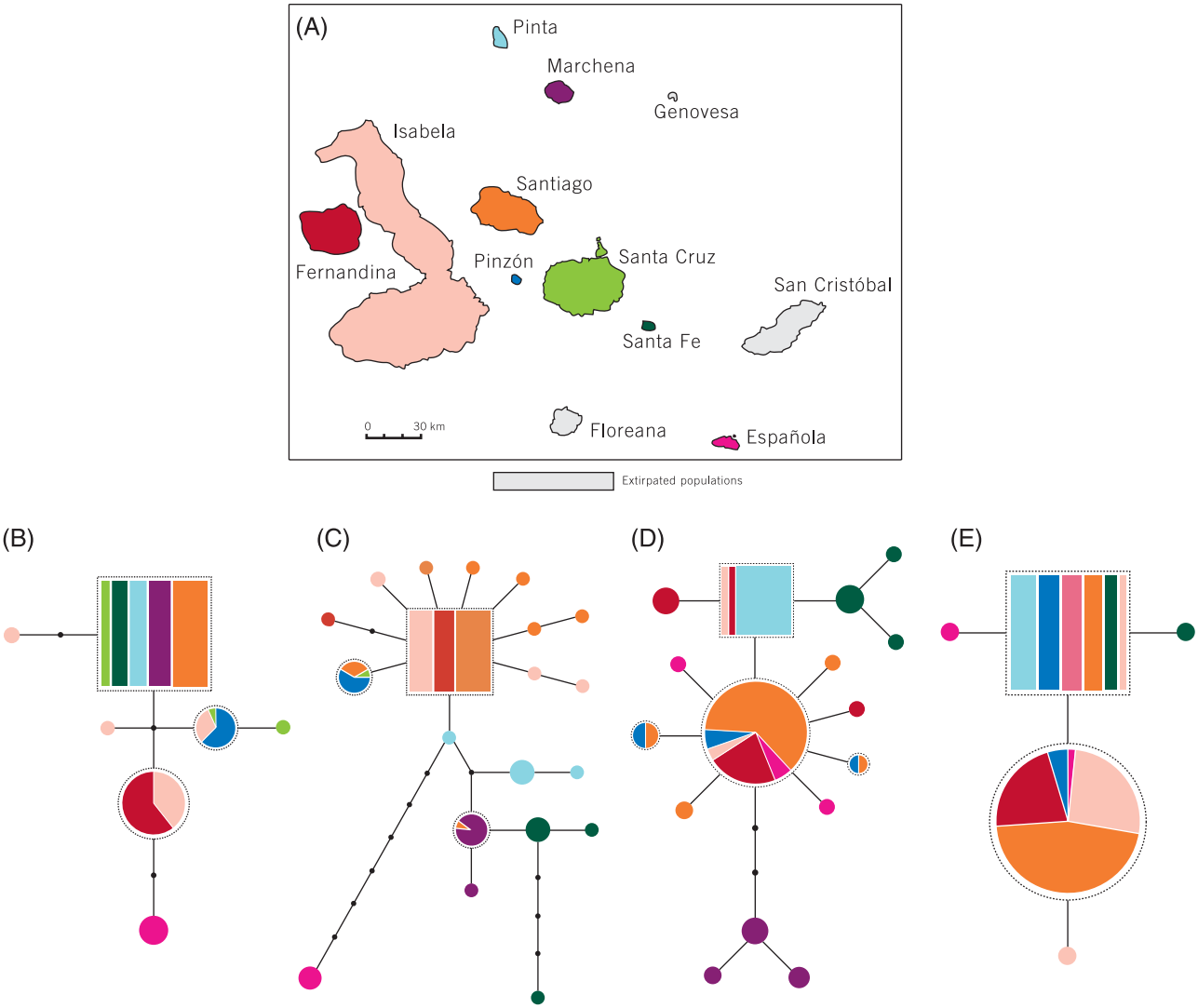

Fig. 1 Map of the Galápagos Islands, Ecuador, where each island population is given a different colour (A). A 95% statistical parsimony haplotype network of combined mtDNA sequence data (3′ COI and CR mtDNA from Bollmer *et al*. 2006) for (B) the Galápagos hawk (*Buteo galapagoensis*) and combined mtDNA sequence data (12S + COI) from each of three ectoparasites species of the Galápagos hawk: (C) *Degeeriella regalis* (D) *Colpocephalum turbinatum* and (E) *Icosta nigra*. Geographical locations are colour-coded in the accompanying map. Each connection (dash) between haplotypes represents one mutational step and small black circles are inferred (unsampled or extinct) haplotypes. Sampled haplotypes are represented by circles or rectangles; squares represent the putative oldest haplotype based on Castelloe & Templeton's (1994) method). If > 1 island populations harboured a haplotype, its frequency in each is indicated by the pie diagrams or the proportionally divided rectangles.

community genetics approach (Wares 2002), allows determination of factors correlated with the microevolutionary histories of co-occurring taxa. Many studies have compared the microevolutionary histories of a single parasite species to one or more host species (Mulvey *et al*. 1991; Dybdahl & Lively 1996; McCoy *et al*. 2003, 2005; Criscione & Blouin 2004; Nieberding *et al*. 2004; Criscione *et al*. 2005, 2006). Studies comparing population histories of co-occurring and distantly related parasite lineages with one another and to their host or hosts, however, are rare.

Study system, conceptual framework and predictions

The Galápagos Islands (Fig. 1A) are a natural evolutionary laboratory (Darwin 1859; Grant *et al*. 1976; Grant & Grant 2006). Volcanic and oceanic in origin, they have never been connected to the mainland. The native Galápagos biota is the most undisturbed of any oceanic archipelago (Tye *et al*. 2002) and because the island system is young, many taxa are in the midst of the speciation process (Caccone *et al*. 2002; Bollmer *et al*. 2005, 2006). Terrestrial ecosystems of

oceanic islands are useful for studying host–parasite interactions because the faunas are simplified relative to mainland faunas (e.g. Perkins 2001; Whiteman *et al*. 2004).

The Galápagos hawk (*Buteo galapagoensis*) is the only resident falconiform and top diurnal predator within the terrestrial ecosystem of the Galápagos Islands (de Vries 1975). As a soaring raptor, it avoids flying over large bodies of water (Fuller *et al*. 1998) and its eight extant island breeding populations are genetically and morphologically distinct (Bollmer *et al*. 2003, 2005, 2006). A population genetic study using nuclear variable number of tandem repeats (VNTRs; Gilbert *et al*. 1990) indicated interisland F_{ST} values were extremely high (Bollmer *et al*. 2005). Interisland gene flow was rare and depended on geographical distance between islands, setting the stage for co-differentiation of the hawk's parasites and the potential for local co-adaptation of parasites (Whiteman *et al*. 2006a). Mitochondrial DNA (mtDNA) sequence data revealed low variation within and high differentiation across the hawk's island populations (Bollmer *et al*. 2006), consistent with the VNTR data (Bollmer *et al*. 2005). The Galápagos hawk is estimated to have diverged from a common ancestor with Swainson's hawk (*Buteo swainsoni*) 126 000 years ago (95% confidence interval 51 000–254 000 years ago; Bollmer *et al*. 2006). Notably, all ectoparasite species found on the Galápagos hawk are also found on the Swainson's hawk (Price *et al*. 2003). Thus, the ectoparasites currently residing on the Galápagos hawk were likely brought to the archipelago from the mainland source population (Bollmer *et al*. 2006). Here, we asked how three relatively phylogenetically unrelated ectoparasite lineages of the Galápagos hawk have responded to the genetic isolation of their only known host in the Galápagos Islands.

We sampled each of the three ectoparasite species across the entire breeding range of *B. galapagoensis*. The three parasite species are phylogenetically independent and have not shared a common ancestor for millennia. Each has been reported exclusively from *B. galapagoensis* within the Galápagos (Clay 1958; Price & Beer 1963; de Vries 1975; Price *et al*. 2003). We gathered data on those natural history traits that are hypothesized to shape parasite microevolution (Nadler 1995; Clayton *et al*. 2004; Huyse *et al*. 2005) (Table 1). Parasites with relatively poor dispersal abilities, vertical transmission, aggregated distributions among hosts, short generation times, high host specificity and small infrapopulation sizes are expected to exhibit relatively high population genetic structure. Parasites with good dispersal abilities, horizontal transmission, uniform distributions among hosts, long generation times, low host specificity and large population sizes are expected to exhibit relatively low population genetic structure (Huyse *et al*. 2005). Clayton *et al*. (2004) found that many of the traits that increase population genetic structure listed above are also found in parasite lineages typified by co-speciation with their hosts.

Table 1 Natural history traits predicted to shape the population structure of three parasite species from 199 Galápagos hawks followed by expected effects of each trait on: (1) parasite population genetic structure among islands, and (2) strength of the relationship between host and parasite population genetic structure. Data from all islands were pooled within each species to illustrate interspecific differences in these factors. The following parameters were calculated in Quantitative Parasitology 3.0 (Reiczigel & Rózsa 2001): prevalence, total number of infected birds/total number of birds sampled; mean abundance, total number of parasite individuals collected/total number of birds sampled; mean intensity, total number of parasite individuals collected/total number of infected birds sampled; the exponent k was calculated following Krebs (1989) and is inversely related to the level of parasite aggregation in the bird component population. Sources for predictions: Clay (1958), Maa (1963); (1969); Price & Beer (1963); Nadler (1995); Price *et al*. (2003); Clayton *et al*. (2004); Whiteman & Parker (2004a, b); Huyse *et al*. (2005) and the present study

Parasite species	Relative dispersal ability	Prevalence	Mean abundance	Exponent k of the negative binomial (directly related to degree of evenness in parasite distribution among host individuals)	Life cycle	Overall predictions for (1) and (2)
Phthiraptera: Ischnocera: *Degeeriella regalis*	Low (1) + (2) + (1) + (2) +	85.4% (79.74–90.02%) (1) + (2) +	14.36 (11.05–17.51) (1) + (2) +	0.48 (1) + (2) +	Direct no free-living stage (1) + (2) +	(1) High (2) High
Phthiraptera: Amblycera: *Colpocephalum turbinatum*	Moderate (1) + (2) +	97.5% (94.23–99.18%) (1) – (2) –	74.59 (58–89.98) (1) – (2) –	0.64 (1) + (2) +	Direct no free-living stage (1) + (2) +	(1) Moderate (2) Moderate
Diptera: Hippoboscidae: *Icosta nigra**	High (1) – (2) –	High* (1) – (2) –	1.49 (1) + (2) +	Evenly distributed* (1) – (2) –	Direct, with free living stage (1) – (2) –	(1) Low (2) Low

*Because individual flies were often collected from multiple host prevalence, intensity and distributional measures were not calculated.

We used all available information to give each parasite species trait values for some of the most important factors believed to shape parasite population structure and degree of tracking of host population structure (Table 1).

The parasites included two species of lice (Insecta: Phthiraptera), *Colpocephalum turbinatum* (Amblycera: Menoponidae) and *Degeeriella regalis* (Ischnocera: Philopteridae). Amblyceran and ischnoceran lice are independently derived from free-living ancestors within the Psocoptera (Johnson *et al*. 2004); members of the two clades are generally distinct in several natural history traits, including overall dispersal ability (Marshall 1981). Transmission between host individuals is thought to be primarily vertical between parents and offspring during brooding in *D. regalis*, while *C. turbinatum* primarily transmits horizontally. Within *B. galapagoensis* populations, the distributions of *C. turbinatum* and *D. regalis* correspond to basic differences in natural history (Table 1; Whiteman & Parker 2004a, b; Whiteman *et al*. 2006a; see Fig. S1, Supplementary material). We also sampled a species of lousefly (Diptera: Hippoboscidae), *Icosta nigra*. The natural history of *I. nigra* is less well known, but it is volant and highly vagile and, like *C. turbinatum*, is found on a number of falconiform hosts on the mainland (Maa 1969). In an important distinction from many lice, hippoboscids have extremely low fecundity (Corbet 1956). Although it is likely that each parasite is restricted to *B. galapagoensis* in the Galápagos Islands (all species are therefore specialists), overall host specificity is generally inversely related to dispersal abilities or ability to establish on new hosts (Clayton *et al*. 2004). Thus, differences in host specificity among these parasite species can be viewed as approximate indicators of dispersal or establishment abilities within a host species and the ecological data we collected corroborate this. In light of variation across the three parasite species in these natural history factors (see Table 1 for specific predictions for each trait), we predicted that *D. regalis* would have the highest degree of population genetic structure, followed by *C. turbinatum* and *I. nigra*. Due to the prevalence of vertical transmission, we also predicted that only *D. regalis* would track the host's pattern of population genetic structure across islands including interisland population divergence times. On the other hand, *C. turbinatum* and *I. nigra* are more likely to be transmitted among unrelated hawk individuals (horizontal transmission). Thus, we predicted that these species would not track host population structure or population divergence times as tightly. We also suggest that the microevolutionary history of the three parasites may be used to create a hypothesis of the host's evolutionary history in the archipelago (Criscione & Blouin 2006; Whiteman & Parker 2005; Kaliszewska *et al*. 2005; Nieberding & Olivieri 2007) because the host's low mitochondrial variation precludes such inferences and the rate of substitution in the parasite exceeds the host's (Hafner *et al*. 1994; Page *et al*. 1998).

Materials and methods

Field methods

We quantitatively sampled ectoparasites from 199 Galápagos hawk individuals across their entire eight island breeding range (Fig. 1A) and from an immature (vagrant) Galápagos hawk in captivity on Santa Cruz, within the Galápagos National Park, Ecuador, between 2001 and 2003 (Table 1). Sampling methods are described elsewhere (Whiteman & Parker 2004a, 2004b; Whiteman *et al*. 2006a). Prevalence and average abundance were compared between parasite species using Quantitative Parasitology 3.0 (Reiczigel & Rózsa 2001). A small blood sample was removed from each host for DNA analysis and stored in lysis buffer (Bollmer *et al*. 2005). In all cases, birds were released unharmed after sampling.

Molecular genetics

We used the voucher method (Cruickshank *et al*. 2001) to extract DNA from individual lice (see Whiteman *et al*. 2006b) and *Icosta nigra* flies (using two legs from each individual) at the University of Missouri-St Louis. DNA extractions from hawks are described elsewhere (Bollmer *et al*. 2005, 2006).

We sequenced homologous regions of mtDNA in all four species (Table 2). However, hawks were invariant at these regions and we also relied on previously published host data sets, including the nuclear multilocus VNTR data set (Bollmer *et al*. 2005) and a variable mtDNA data set (Bollmer *et al*. 2006) for comparative analyses.

Parasite

For each of the three parasite species, only a single parasite was genotyped from a single host individual (Table 2). The primer pair LCO1490 and HCO2198 was used to amplify through polymerase chain reaction (PCR) and sequence part of the mitochondrial gene cytochrome *c* oxidase subunit I (COI, near the 5′ end; Folmer *et al*. 1994) following Whiteman *et al*. (2006b). We also amplified and sequenced a fragment of 12S mitochondrial ribosomal RNA from the same samples using the primer pair 12SAI and 12SBI (Simon *et al*. 1994) following Whiteman *et al*. (2006b). Direct sequencing of both strands was performed on Applied Biosystems 3730xl DNA Analysers (Applied Biosystems) by Macrogen or on an Applied Biosystems 377 DNA Analyser at the University of Missouri-St Louis.

Host

Amplification and sequencing of the 5′ COI fragment from Galápagos hawks is described elsewhere (Bollmer *et al*.

Table 2 Host and parasite mtDNA accessions (combined COI + 12S data set), sample sizes, and population genetic parameters

			Population genetic parameters				
Species	Island	*N*	Polymorphic sites	Haplotypes	Haplotype diversity	Nucleotide diversity	Theta-*W*, per sequence
Parasite:	Española	7	0	1	0	0	0
Degeeriella regalis	Fernandina	13	2	2	0.154	0.00028	0.645
	Isabela	18	2	4	0.399	0.00029	0.582
	Marchena	13	2	2	0.154	0.00014	0.322
	Pinta	10	3	3	0.378	0.00055	1.06
	Pinzón	7	0	1	0	0	0
	Santa Fe	11	1	3	0.346	0.00017	0.341
	Santiago	31	8	8	0.536	0.00068	2
Parasite:	Española	5	2	3	0.7	0.00084	0.96
Colpocephalum turbinatum	Fernandina	23	2	3	0.66	0.00102	0.542
	Isabela	7	2	3	0.67	0.0009	0.816
	Marchena	13	2	3	0.641	0.00078	0.645
	Pinta	24	0	1	0	0	0
	Pinzón	7	2	3	0.714	0.0009	0.816
	Santa Fe	10	2	3	0.378	0.00042	0.707
	Santiago	38	4	5	0.333	0.00038	0.952
Parasite:	Española	13	1	3	0.275	0.0003	0.629
Icosta nigra	Fernandina	14	0	1	0	0	0
	Isabela	19	2	3	0.205	0.00022	0.572
	Pinta	15	0	1	0	0	0
	Pinzón	14	0	2	0.363	0.00039	0.315
	Santa Fe	5	1	2	0.4	0.00043	0.48
	Santiago	37	1	2	0.315	0.00034	0.240
Host:	Española	9	0	1	0	0	0
Buteo galapagoensis	Fernandina	10	0	1	0	0	0
	Isabela	10	0	1	0	0	0
	Marchena	10	0	1	0	0	0
	Pinta	11	0	1	0	0	0
	Pinzón	10	0	1	0	0	0
	Santa Fe	9	0	1	0	0	0
	Santiago	11	0	1	0	0	0

2006). The 12S primers used were L1753 and H2294 from Sorenson *et al*. (1999). Single-stranded sequences from hawks were obtained using ABI BigDye Terminator version 3.1 and an ABI PRISM 3100-Avant genetic analyser (PE Applied Biosystems; University of Florida). A subset of individuals was sequenced in both directions.

Phylogeographical, population genetic, and coalescent analyses

Raw sequence chromatograms of forward and reverse strands were evaluated by eye and assembled for each amplicon in Seqman II (DNASTAR). Consensus sequences were aligned in the SE-AL program (Rambaut 1996) or in CLUSTAL_X program (Thompson *et al*. 1997). We examined the original chromatograms to ensure that variable sites were unambiguously assigned. Sequences have been deposited in GenBank: *Degeeriella regalis* (DQ490701–DQ490720), *Colpocephalum turbinatum* (EF201985–EF202000) and *I. nigra* (EF2020001–EF202006). *Buteo galapagoensis* accession numbers were AY870866 and DQ485965. Haplotypes refer to combined COI + 12S sequences.

We were interested in understanding how haplotypes within each species were related (temporal information) and how these haplotypes were distributed across the archipelago (spatial information). While traditional *F*-statistics (Wright 1951) yield useful information on variation in allele frequencies within and between populations, these summary statistics do not yield genealogical information (gene genealogies). Statistical parsimony networks are particularly useful for inferring and visualizing genealogical relationships among DNA sequences that have diverged recently. While phylogenetic analysis assumes that ancestors are extinct, statistical parsimony network analysis does not, and frequently ancestral (interior) haplotypes are extant. Tip (outer) haplotypes are interpreted as

Table 3 Population genetic parameters of two homologous mtDNA regions sequenced across island populations of three ectoparasite species. Species are listed according to the level of overall genetic diversity and population structure (highest–lowest)

Species	Population genetic parameters	5′ COI	3′ 12S	5′ COI +3′ 12S
Parasite:	Aligned length	603 bp	496 bp	1099 bp
Degeeriella regalis	No. of polymorphic sites	13	15	28
(N = 111	Nucleotide diversity	0.00284	0.00114	0.00207
from nine populations)	No. of haplotypes	10	12	20
	Haplotype diversity	0.627	0.692	0.783
	Theta per sequence from S (Watterson's estimator)	2.465	1.515	3.976
	No. of synonymous/nonsynonymous mutations	9/4 (200 codons)	—	—
	Average interisland pairwise genetic distance (K_2P)	2.37	1.51	3.12
Parasite:	Aligned length	601 bp	349 bp	950 bp
Colpocephalum turbinatum	No. of polymorphic sites	8	9	17
(N = 127	Nucleotide diversity	0.00168	0.00178	0.00171
from eight populations)	No. of haplotypes	8	10	16
	Haplotype diversity	0.635	0.496	0.769
	Theta per sequence from S (Watterson's estimator)	1.477	1.661	3.138
	No. of synonymous/nonsynonymous mutations	6/2 (199 codons)	—	—
	Average interisland pairwise genetic distance (K_2P)	0.91	0.55	1.47
Parasite:	Aligned length	612 bp	325 bp	937 bp
Icosta nigra	No. of polymorphic sites	1	3	4
(N = 117	Nucleotide diversity	0.00003	0.00163	0.00058
from eight populations)	No. of haplotypes	2	4	5
	Haplotype diversity	0.00028	0.00035	0.520
	No. of synonymous/nonsynonymous mutations	1/0 (203 codons)	—	—
	Theta per sequence from S (Watterson's estimator)	0.187	0.562	0.750
	Average interisland pairwise genetic distance (K_2P)	0	0.42	0.42

K_2P, Kimura 2-parameter.

being younger than (and possibly derived from) interior haplotypes (Castelloe & Templeton 1994). Four 95% statistical parsimony haplotype networks were constructed using TCS 1.8 (Clement *et al*. 2000) for the combined COI + 12S data set from each parasite species and the variable mtDNA data set (Bollmer *et al*. 2006) from *B. galapagoensis*. This algorithm also allows inference of potentially the oldest haplotype based on positional and frequency data. Because the gene regions were both mitochondrial and are assumed to be in complete linkage disequilibrium (cf. Gatenbein *et al*. 2005) and separate analyses for each gene region were consistent with the combined data set (but yielded less information separately than in the combined analysis), we chose to display networks and perform most subsequent population genetic analyses using the combined data set.

We calculated standard population genetic parameters (Table 3) for COI and 12S (and combined data set) in DNASP (Rozas & Rozas 1999). For each parasite species, ARLEQUIN 2.01 (Schneider *et al*. 2000) was used to partition genetic variance components among and within-island populations using analysis of molecular variance (AMOVA; Excoffier *et al*. 1992) and compare associated Φ_{ST} values among species. This F_{ST} analogue Φ_{ST} is equal to the ratio of the genetic variance component due to differences among populations over the estimated total variance within the species for each species (Excoffier *et al*. 1992). The significance of co-variance components was tested using non-parametric permutation procedures in ARLEQUIN 2.01. We also calculated interisland F_{ST} values (the proportion of genetic variation in the total population due to differences between subpopulations) in ARLEQUIN 2.01, using Kimura 2-parameter genetic distances. The significance of F_{ST} values was tested by permuting haplotypes between populations in ARLEQUIN 2.01. Host VNTR F_{ST} values were obtained from Bollmer *et al*. (2005), which included individual hosts of parasites sequenced in the present study. We did not use pairwise F_{ST} values from the host mtDNA, because values were typically either 0 or 1, reflecting the extremely low mtDNA diversity. We tested for isolation by distance (Rousset 1997) in each parasite by using a Mantel (1967) test in ARLEQUIN 2.01 with 10 000 permutations. In our largest data sets, we made 28 interisland comparisons. To account for the statistical effects of multiple comparisons, we reduced the alpha level to 0.002 for these and similar analyses described below (Rice 1989). To determine if parasites were tracking host interisland gene flow, we used a Mantel test in ARLEQUIN to compare the interisland F_{ST} matrix of each parasite species to a matrix of the host's interisland VNTR F_{ST} values. We also used partial Mantel

tests in ARLEQUIN 2.01, which hold one matrix (geographical distance or host F_{ST} values) constant when testing for an association between two other matrices. Partial Mantel tests are controversial, however, and were only used to further explore results from the Mantel tests (Raufaste & Rousset 2001). We used nonparametric Kendall's *W*-test in SPSS version 12.0 to compare the magnitudes of each interisland F_{ST} value among each parasite species.

Historical variation in population size should be correlated if the host and parasite population histories are tightly linked. Island area and within-island population nuclear genetic diversity (from VNTRs) were directly related in the host (Bollmer *et al*. 2005). Thus, we used a Pearson's correlation procedure in SPSS version 12.0 to determine if the island-level nuclear genetic diversity of the host (using VNTR heterozygosity values from Whiteman *et al*. 2006a) and genetic diversity values from each parasites species (haplotype diversity, nucleotide diversity and θ, estimated using DNASP) across each island were correlated across the archipelago.

The haplotype networks indicated that haplotypes were often found on multiple islands. This may be explained by the presence of recent gene flow among islands or retained ancestral haplotypes (polymorphisms) on multiple islands. To differentiate between incomplete lineage sorting (retained ancestral polymorphisms) and interisland gene flow and to complement our analyses above, we used the Markov chain Monte Carlo coalescent modelling program MDIV (Nielsen & Wakeley 2001), which estimates maximum-likelihood population sizes (θ = theta = $2N_{ef}\mu$), migration rates between populations ($N_{ef}m$), and a population divergence time parameter ($T = t/N_{ef}$), using the combined mtDNA data sets for each of the parasites and the variable mtDNA data set for the host (Bollmer *et al*. 2006). Because rates of gene flow and divergence times between populations covary, this method calculates the posterior probability of each parameter given the gene genealogy. Relative divergence times were calculated by taking the product of the divergence time parameter and θ to control for differences in population size. Insertions and deletions in the 12S regions were coded transversions because MDIV does not allow consideration of gaps (Barrowclough *et al*. 2005). We used the finite sites Hasegawa–Kishino–Yano (HKY) substitution model and a priori maxima were set for *M* and *T*, with $M_{max} = 5$ or 10, and $T_{max} = 10$. These values were chosen because the host showed high genetic differentiation across its range and the arrival of the hawk in the archipelago was < 300 000 years before present (Bollmer *et al*. 2006). Pairwise, interisland θ values (per sequence) were estimated in MDIV from the data. Simulations were run twice (with different random seeds) for each pairwise comparison, with 2 000 000 generations and a 500 000-generation burn in. The parameter values corresponding to the modes of the likelihood distributions were the point estimates for each parameter (θ, *M*, and *T*). We did not convert the time estimates to years before present because there are no published estimates of ischnoceran, amblyceran or hippoboscid mtDNA substitution rates. Nonetheless, the divergence dates (the product of θ and *T*) remain inferential tools in a relative context. Because we were also interested in determining if each parasite species co-diverged with the host across islands during colonization in the Galápagos, we used Mantel tests (with 10 000 permutations in ARLEQUIN 2.01) to determine if divergence times of host and each of the parasite species were related to interisland geographical distances and whether the relative host and parasite divergence times were correlated. As above, we used partial Mantel tests to hold either host population divergence times or geographical distance matrices constant. We used nonparametric Kendall's *W*-test in SPSS version 12.0 to compare the magnitudes of interisland gene flow values across the three parasites.

Results

Parasite collections and distributions

We collected a total of 14 843 individuals of the louse *Colpocephalum turbinatum* and 2858 individuals of the louse *Degeeriella regalis* from 199 Galápagos hawks across all eight host populations. We collected 296 *Icosta nigra* individuals from seven host populations (no flies were recovered from Isla Marchena despite sampling about one-fourth of this hawk population; Bollmer *et al*. 2005). We also found lice of both species from two nestling hawks near fledging-age on Isla Fernandina, indicating that both louse species undergo vertical transmission (Whiteman & Parker 2004a). The basic quantitative descriptors of parasite load from each island population are given in Table 1. Notably, *C. turbinatum* was significantly more prevalent, abundant, and was more evenly distributed within the hawks than *D. regalis* (all $P < 0.001$). Because *I. nigra* abundance values were difficult to quantify, we only present prevalence values. *I. nigra* was highly prevalent in all hawk populations where present, though abundance values were low relative to lice, consistent with Maa's (1969) observation.

Phylogeographical, population genetics, and coalescent analyses

Approximately 1 kb of mtDNA sequences (COI + 12S) was obtained from 111 *D. regalis* individuals (eight populations +1 from the juvenile Santa Cruz bird), 127 *C. turbinatum* individuals (eight populations) and 117 *I. nigra* individuals (seven populations) (Table 2) from the 199 hawks sampled. The 81 host individuals sequenced at both loci (from the 199 sampled) did not harbour any genetic variability within- or across-island populations (Table 2).

Table 4 Hierarchical analysis of molecular variance for mitochondrial haplotypes from three ectoparasite species partitioned by geography

Species	Partition	d.f.	% variation	Φ_{ST}	*P*
Degeeriella regalis	Among-island populations	7	84.76	0.85	< 0.00001
	Within-island populations	102	15.24	—	—
Colpocephalum turbinatum	Among-island populations	7	72.86	0.73	< 0.00001
	Within-island populations	119	27.14	—	—
Icosta nigra	Among-island populations	6	63.27	0.63	< 0.00001
	Within-island populations	111	36.73	—	—

The mtDNA network from the host (Fig. 1B) reveals some population subdivision with respect to geography (all individuals in four island populations were fixed), but a much higher degree of population subdivision correlated with geography is apparent in *D. regalis* and *C. turbinatum* mtDNA networks (Fig. 1C,D). The *I. nigra* network was similar to the host in this respect (Fig. 1E) and variation within *I. nigra* sequences was low. For *D. regalis*, the Española population was the most highly differentiated from the others (Fig. 1C), which was also the case for the host (Fig. 1B; Bollmer *et al*. 2006). Moreover, the five most inbred and smallest island populations of hawks (Española, Marchena, Pinta, Pinzón, and Santa Fe) harboured highly differentiated and unique *D. regalis* mtDNA haplogroups. Each parasite species harboured island-exclusive (private) haplotypes, with the largest number in *D. regalis* (17 in all eight island populations), followed by *C. turbinatum* (12 in five island populations), *I. nigra* (three in three island populations) and the host (none in the homologous mtDNA sequence data set and four in three island populations in the variable (expanded) mtDNA data set from Bollmer *et al*. 2006).

Degeeriella regalis sequences were the most variable followed by *C. turbinatum* and *I. nigra* (Table 3). The total number of polymorphic (segregating) sites was very similar in the two louse species, and very low overall in the lousefly (Table 3). Populations of each parasite species showed significant genetic differentiation across islands. AMOVA results (Table 4) indicate that the among-population component was the strongest predictor of genetic partitioning in each parasite, with *D. regalis* being the most differentiated among islands, followed by *C. turbinatum* and *I. nigra*. Of 28 interisland pairwise comparisons of *D. regalis* F_{ST} values, 89.3% were significantly differentiated, while 71.4% of *C. turbinatum* F_{ST} comparisons and 57.1% of *I. nigra* F_{ST} comparisons were significantly greater than zero (see Tables S1–S3). For the 21 interisland comparisons where F_{ST} values from all three parasites were available (all comparisons except those including Marchena), F_{ST} values between each pair of islands (where all parasite species were present) were significantly different among the parasite species (*I. nigra* mean rank = 1.71; *C. turbinatum* mean rank = 1.81; *D. regalis* mean rank = 2.48) (Kendall's $W = 0.172$; $\chi^2 = 7.24$; $P < 0.05$). Similarly, average pairwise interisland genetic distances of mtDNA were highest in *D. regalis*, followed by *C. turbinatum* and *I. nigra* (Table 3). Overall (archipelago-wide) θ values were highest for *D. regalis*, followed by *C. turbinatum* and *I. nigra*.

A significant correlation between interisland F_{ST} values and geographical distance was found in *D. regalis* but not *C. turbinatum* or *I. nigra* (Table 5). A significant and positive correlation was found between parasite interisland F_{ST} values and the host VNTR F_{ST} values for *D. regalis* and *C. turbinatum* (Table 5). There was a positive but nonsignificant relationship between *I. nigra* interisland F_{ST} values and the host VNTR F_{ST} values (Table 5). The results of the partial Mantel tests were in accord with the Mantel tests and indicate that variation in *D. regalis* F_{ST} values were independently and positively related to geographical distance and host VNTR F_{ST} values (Table 5); no significant relationship was found for the other two parasites. However, the relationship between each of the other two parasites' interisland F_{ST} values and host VNTR F_{ST} values was positive and approached significance ($P = 0.09$ in both cases) while holding geographical distance constant.

The host's nuclear genetic diversity (island-level heterozygosity from VNTRs reported in Whiteman *et al*. 2006a) was significantly related to island-level mtDNA nucleotide diversity ($R = 0.758$, $P < 0.05$) and mtDNA θ-W ($R = 0.724$, $P < 0.05$) in *D. regalis* but not in *C. turbinatum* ($R = –0.082$, $P > 0.05$; $R = –0.214$, $P > 0.05$) or *I. nigra* ($R = –0.326$, $P > 0.05$; $R = –0.100$, $P > 0.05$). Mitochondrial DNA haplotype diversity and host heterozygosity were unrelated in each parasite species (*D. regalis*: $R = 0.554$, $P > 0.05$; *C. turbinatum*: $R = –0.239$, $P > 0.05$; *I. nigra*: $R = –0.322$, $P > 0.05$).

A positive correlation between interisland divergence time values (reported as the product of T_{div} and θ between each population) and interisland geographical distance was found for *D. regalis* and the host ($R = 0.63$; $P = 0.07$), but not for *C. turbinatum* or *I. nigra* (Table 5). A positive correlation between parasite and host interisland population divergence time values was found for *D. regalis*, but not for *C. turbinatum* or *I. nigra* (Table 5; Fig. 1A–C). The results of the partial Mantel tests were in accord with the Mantel tests and indicate that variation in *D. regalis* population divergence time values were independently and positively related

Table 5 Results of Mantel and partial Mantel tests for significant correlations between interisland parasite mtDNA F_{ST} or parasite mtDNA population divergence time values vs. interisland geographical distance, host nuclear F_{ST} values from VNTRs and host mtDNA population divergence times across eight island populations for *Degeeriella regalis* and *Colpocephalum turbinatum* and seven island populations for *Icosta nigra*. For partial Mantel tests, parentheses indicate which factor was removed from the analysis

Matrix comparison	*r*	*P* value
D. regalis mtDNA–geographical distance	0.61	< 0.001
D. regalis mtDNA–host nuclear DNA	0.73	< 0.001
D. regalis mtDNA population divergence time–geographical distance	0.74	< 0.05
D. regalis mtDNA population divergence time–host mtDNA population divergence time	0.77	< 0.05
D. regalis mtDNA–geographical distance_ (host nuclear DNA)	0.23	0.21
D. regalis mtDNA–host nuclear DNA_ (geographical distance)	0.55	< 0.01
D. regalis mtDNA population divergence time–geographical geographical distance_(host mtDNA population divergence time)	0.51	< 0.05
D. regalis mtDNA population divergence time–host mtDNA population divergence time_(geographical distance)	0.59	< 0.05
C. turbinatum mtDNA–geographical distance	0.30	0.16
C. turbinatum mtDNA–host nuclear DNA	0.49	< 0.05
C. turbinatum mtDNA population divergence time–geographical distance	–0.15	0.65
C. turbinatum mtDNA population divergence time–host mtDNA population divergence time	–0.35	0.91
C. turbinatum mtDNA–geographical distance_(host nuclear DNA)	–0.05	0.56
C. turbinatum mtDNA–host nuclear DNA_(geographical distance)	0.41	0.09
C. turbinatum mtDNA population divergence time–geographical distance_(Host mtDNA population divergence time)	0.10	0.32
C. turbinatum mtDNA population divergence time–host mtDNA population divergence time_(geographical distance)	0.34	0.91
I. nigra mtDNA–geographical distance	–0.05	0.61
I. nigra mtDNA–host nuclear DNA	0.20	0.27
I. nigra mtDNA population divergence time–geographical distance	–0.15	0.68
I. nigra mtDNA population divergence time–host mtDNA population divergence time	–0.19	0.76
I. nigra mtDNA–geographical distance_(host nuclear DNA)	–0.26	0.82
I. nigra mtDNA–host nuclear DNA_(geographical distance)	0.32	0.09
I. nigra mtDNA population divergence time–geographical distance_(host mtDNA population divergence time)	–0.04	0.55
I. nigra mtDNA population divergence time–host mtDNA population divergence time_(geographical distance)	–0.13	0.66

r, correlation coefficient.

to geographical distance and host population divergence time values (Table 5). No significant relationship was found for the other two parasites.

Coalescent estimates of parasite gene flow among islands were concordant with F_{ST} values between islands (see Supplementary material). For the 21 interisland comparisons where estimates from all three parasites were available, gene flow levels were significantly different among parasite species. The highest levels of interisland gene flow for each interisland comparison was found for *I. nigra*, then *C. turbinatum* and *D. regalis* (*I. nigra* mean rank = 2.48; *C. turbinatum* mean rank = 2.10; *D. regalis* mean rank = 1.43) (Kendall's $W = 0.303$; $\chi^2 = 12.718$; $P < 0.01$).

This analysis also shows that although time since *D. regalis* island population divergence increases in a positive, linear fashion with geographical distance between islands, some *D. regalis* island populations that diverged relatively long ago have been recently connected by gene flow. The T_{div} estimate of *D. regalis* populations inhabiting Santiago and Marchena was 2.56 time units and a *D. regalis* female was estimated to have moved between these populations every 8.3 generations, contrasting with a female migration event migration rate every 83.3 generations between Santiago and Santa Fe, which had a similar divergence date (3.17 time units) to that of Santiago and Marchena (see Supplementary material). Thus, the migration rate of *D. regalis* between Santiago and Marchena was > 10 times higher than between Santiago and Santa Fe.

Discussion

Patterns of genetic isolation across parasite species

Population genetic and phylogeographical studies of co-occurring parasites and their common hosts shed light on the processes underlying parasite diversification (Nadler 1995; Huyse *et al*. 2005). Although similar patterns of genetic isolation are expected in species with similar natural histories (e.g. Barber *et al*. 2006), a community genetics approach also allows insight into how divergence in natural history traits shape microevolutionary processes of co-occurring species (Criscione & Blouin 2004). In this study, the degree of population genetic, phylogeographical structure and co-divergence with the host varied for each parasite species in ways that were predicted by the parasites' ecology. *Degeeriella regalis* harboured the most genetic variation overall, was the most structured and divergent among islands and had the lowest levels of gene flow among

islands, followed by *Colpocephalum turbinatum*, and *Icosta nigra*. Notably, the host was completely invariant at two mitochondrial regions that were comparatively variable in each of the parasite species. While *D. regalis* average abundances were significantly lower than *C. turbinatum*, the overall θ values were higher for *D. regalis*, reflecting the fact that effective population size across populations should increase with increasing genetic differentiation. Because *D. regalis* infrapopulations are, on average, smaller than those of *C. turbinatum* and prevalence of *C. turbinatum* is higher than those of *D. regalis*, the effects of genetic drift are likely to be stronger in *D. regalis* at these mitochondrial loci.

The amount of *D. regalis* gene flow among islands (in the form of F_{ST} values) was positively correlated with the nuclear gene flow of the host (using VNTR F_{ST} values), while this correlation was weaker for *C. turbinatum* and absent for *I. nigra*. These patterns are consistent with the fact that dispersal between host individuals is lowest for *D. regalis*, higher for *C. turbinatum* and highest for the volant *I. nigra.* The coalescent estimates of relative divergence times of *D. regalis* and the host's island populations were each correlated with distance. These divergence time estimates were also positively related between *D. regalis* and the host (independent of the relationship with geographical distance), suggesting that *D. regalis* tracked the host's genealogical history in the archipelago, a hypothesis that fits well with its largely vertical mode of transmission (Whiteman & Parker 2004a). Congruence in both population connectivity and genealogical history (temporal congruence) between *D. regalis* and its host also suggests that the two taxa responded similarly to shared biogeographical events (Cunningham & Collins 1994) that took place within that last 250 000 years (based on the split between Galápagos and Swainson's hawks). The evolutionary history of *D. regalis* within the archipelago is likely to be dependent on both host gene flow and colonization history to a greater degree than the two other parasites. These findings illuminate the potential importance of association by descent (or vertical transmission across host individuals, populations, lineages or species; Brooks 1979; Page 2003; for *D. regalis*) and association by colonization (or horizontal transmission across host individuals, populations, lineages or species; *C. turbinatum* and *I. nigra*) in driving macroevolutionary patterns of parasite diversification (Hoberg *et al*. 1997). Current coalescent methods (including MDIV) permit joint estimation of migration rates and population divergence times only between two populations. In this eight-island host–parasite system, several island populations of each species are likely exchanging migrants. It is possible that the strong pattern of isolation by distance found for *D. regalis* and *B. galapagoensis* may have biased the estimates of population divergence times leading to the positive relationship between pairwise interisland divergence times of *D. regalis* and *B. galapagoensis*. High levels of migration among populations may render estimation of divergence times between two populations difficult (Wakeley 2000). However, several studies with similar findings (multiple populations exchanging migrants and strong isolation by distance) have shown that jointly estimated divergence times were reasonable and consistent with independent information (Smith & Farrell 2005; Steeves *et al*. 2005). Because the coalescent estimates used only a single, nonrecombining marker, the results should be interpreted with caution until more markers and coalescent methods allowing for simultaneous comparisons of multiple populations become available.

Incipient allopatric speciation, hypothesized to play an important role in parasite diversification (Clay 1949; Huyse *et al*. 2005) may be occurring in *D. regalis* and *C. turbinatum* within the Galápagos. Population differentiation in amblyceran (Barker *et al*. 1991a, b) and ischnoceran lice (Nadler *et al*. 1990; Lymbery & Dadour 1999) has been described previously although not explicitly in relation to host population genetic structure. Despite their very different natural histories from ischnocerans, there was an effect of host population subdivision on the population genetic structure of *C. turbinatum*, although this was not strongly related to host gene flow or isolation by distance. The larger population size of *C. turbinatum* relative to *D. regalis* may be one factor that increases coalescence time even though the latter may be tracking host gene flow (Rannala & Michalakis 2003). Variation in mtDNA within *D. regalis* island populations was positively correlated with the host's nuclear diversity, suggesting that population histories of the two species may be linked. These findings are also consistent with the hypothesis that some characteristics of the 'island syndrome' extend to ectoparasites as well as endoparasites (Nieberding *et al*. 2006).

The *I. nigra* population within Galápagos harboured relatively low mitochondrial variation. Although there was significant differentiation among its populations, the coalescent modelling showed that gene flow was highest for *I. nigra* among the three parasite species. A similar pattern of low diversity and weak population differentiation was observed in the related tsetse fly (*Glossina pallidipes*) in Africa (Gooding & Krafsur 2005), which underwent a severe and recent population bottleneck (Krafsur 2002). Population sizes of *I. nigra* are also much smaller than those of the two louse species. Finally, differences in substitution rate may also underlie the low overall variation observed in the flies. Ischnoceran and amblyceran lice have accelerated rates of mitochondrial evolution relative to other Psocoptera (Yoshizawa & Johnson 2003), whereas parasitic flies tend not to have an accelerated rate of mitochondrial evolution relative to nonparasitic flies (Castro *et al*. 2002).

Host–parasite studies at the macroevolutionary scale have advanced biomedical and evolutionary research by providing a robust statistical framework for studying

parallel evolutionary histories of distantly related taxa over vast expanses of time. Nonetheless, such studies may not reveal the processes that created the patterns. This comparative host–parasite co-evolutionary study adds to the growing body of evidence that parasite natural history and epidemiological parameters are key in mediating this process (Johnson *et al*. 2002; Criscione & Blouin 2004).

Implications for conservation management

The observed pattern of local differentiation within and recurrent gene flow between populations may facilitate local adaptation by these ectoparasites (Gandon *et al*. 1996). Host races of parasites may have formed in the same populations where the host exhibited low genetic diversity and weak innate immune responses (Whiteman *et al*. 2006a). The level of parasite gene flow among genetically structured parasite populations is directly related to the ability of the parasites to adapt locally to hosts (Lively 1999; Morgan *et al*. 2005) and the introduction of novel parasite alleles into the smallest hawk populations may increase parasite virulence. We recommend against moving hawk individuals among islands that currently harbour hawk populations. Future studies should examine the breeding systems of these ectoparasites, including fine-scale parasite gene flow within and between members of hawk social groups (Whiteman & Parker 2004a; Leo *et al*. 2005).

The smallest and most inbred hawk populations also harboured highly differentiated *D. regalis* populations and, like the host, *D. regalis* exhibits isolation by distance between islands. This reinforces the interpretation based on nuclear VNTRs from the hawk that the smallest of the hawk's island populations are on relatively independent evolutionary trajectories (Bollmer *et al*. 2005). The mtDNA data set from this parasite was more variable than the host's, and its mitochondrial gene flow was correlated with the host's nuclear gene flow and mtDNA-based population divergence times (where detectable in the host data set) while controlling for isolation by distance between islands. Thus, *D. regalis* is a good candidate for use as a proxy (Nieberding & Olivieri 2007) conservation genetics tool in understanding the host's recent evolutionary history. While the hawks of Marchena, Pinta, Santa Fe and Santiago shared a single mitochondrial haplotype, there are clear genealogical relationships among-island populations in the *D. regalis* data set that may be used to generate a hypothesis of the host's phylogeographical history that does not contradict information derived directly from the host. The island populations of Marchena and Santa Fe appear to be very closely related and these two populations are in turn relatively closely related to the Pinta population. The island populations of Santiago, Isabela and Fernandina are closely related, as are the populations of Santiago, Santa Cruz, and Pinzón. The population (based on host and *D. regalis* mitochondrial data) on Española is the most differentiated. This could warrant special consideration in a conservation management plan (Tye *et al*. 2002). Genetic studies and distributions of other Galápagos taxa show a similar pattern of high endemism on Española (Finston & Peck 1997; Kizirian *et al*. 2004; Parent & Crespi 2006). This is consistent with the fact that it is situated in the southeast of the archipelago and is the most windward of all the islands (Lea *et al*. 2006). We suggest that conservation managers cautiously use *D. regalis* genetic data as an approximate management guide, along with direct information from the host (Bollmer *et al*. 2005, 2006), if captive breeding or repatriation programs (e.g. Hofkin *et al*. 2003) become necessary in this declining species.

Although isolation of *B. galapagoensis* and *D. regalis* island populations appears clear, rare interisland movement of hawks has been documented using banded *B. galapagoensis* individuals and the VNTR and mitochondrial genotyping studies (Bollmer *et al*. 2005, 2006). One *D. regalis* specimen from a territorial adult male hawk was sampled on Santiago, yet had the *D. regalis* haplotype common on birds sampled on Marchena (Fig. 1B,C); this was most likely the result of recent migration of *D. regalis* from Marchena to Santiago rather than the retention of an ancestral haplotype. Thus, parasite genotypes can provide an additional way to document rare dispersal or gene flow events. Some immature birds sampled on Santa Cruz were immigrants from neighbouring islands, based on genotyping studies (Bollmer *et al*. 2006). Territorial adult hawks physically attack immature hawk individuals, and immatures also form social groups in which they interact physically. During such encounters, easily transmitted parasites (*C. turbinatum* and *I. nigra*) might move between hosts (McCoy *et al*. 2003), and this may be exacerbated because immature hawks have significantly higher parasite abundances than territorial adult hawks (Whiteman & Parker 2004b). The genetic patterns of *C. turbinatum* and *I. nigra* likely reflect the dispersal of their hawk hosts between islands and possibly the movements of other host species (see Whiteman & Parker 2004a), although host-specific adaptations may constrain some ectoparasites from colonizing novel hosts (Balakrishnan & Sorenson 2007). An important caveat is that only a matrilineal marker was employed in each of the parasite species and these data reflect the history of the mitochondrial genome and not necessarily the species or populations. Further insight into the recent evolutionary histories of these parasites would be gained by using nuclear markers to complement the data presented above.

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References

Balakrishnan CN, Sorenson MD (2007) Dispersal ecology versus host specialization as determinants of ectoparasite distribution in brood parasitic indigobirds and their estrilid finch hosts. *Molecular Ecology*, **16**, 217–229.

Barber PH, Palumbi SR, Erdmann MV (2006) Comparative phylogeography of three co-distributed stomatopods: origins and timing of regional lineage diversification in the coral triangle. *Evolution*, **60**, 1825–1839.

Barker SC, Briscoe DA, Close RL, Dallas P (1991a) Genetic variation in the *Heterodoxus octoseriatus* group (Phthiraptera): a test of Price's model of parasite evolution. *International Journal for Parasitology*, **21**, 555–563.

Barker SC, Close RL, Briscoe DL (1991b) Genetic divergence in *Heterodoxus octoseriatus* (Phthiraptera). *International Journal for Parasitology*, **21**, 479–482.

Barrowclough GF, Groth JG, Mertz LA, Guitérrez RJ (2005) Genetic structure, introgression, and a narrow hybrid zone between northern and California spotted owls (*Strix occidentalis*). *Molecular Ecology*, **14**, 1109–1120.

Bollmer JL, Kimball RT, Whiteman NK, Sarasola JH, Parker PG (2006) Phylogeography of the Galápagos Hawk (*Buteo galapagoensis*): a recent arrival to the Galápagos Islands. *Molecular Phylogenetics and Evolution*, **39**, 237–247.

Bollmer JL, Sanchez T, Donaghy Cannon M *et al*. (2003) Variation in morphology and mating system among island populations of Galápagos hawks. *Condor*, **105**, 428–438.

Bollmer JL, Whiteman NK, Bednarz JC, de Vries T, Parker PG (2005) Population genetics of the Galápagos hawk: genetic monomorphism within isolated populations. *Auk*, **122**, 1210–1224.

Brooks DR (1979) Testing hypotheses of evolutionary relationships among parasites: the Digeneans of Crocodilians. *American Zoologist*, **19**, 1225–1238.

Caccone A, Gentile G, Gibbs JP *et al*. (2002) Phylogeography and history of giant Galápagos tortoises. *Evolution*, **56**, 2052–2066.

Castelloe J, Templeton AR (1994) Root probabilities for intraspecific gene trees under neutral coalescent theory. *Molecular Phylogenetics and Evolution*, **3**, 102–113.

Castro LR, Austin AD, Dowton M (2002) Contrasting rates of mitochondrial molecular evolution in parasitic Diptera and Hymenoptera. *Molecular Biology and Evolution*, **19**, 1100–1113.

Clay T (1949) Some problems in the evolution of a group of ectoparasites. *Evolution*, **3**, 279–299.

Clay T (1958) Revisions of Mallophaga genera. *Degeeriella* from the Falconiformes. *Bulletin of the British Museum of Natural History, Entomology*, **7**, 121–207.

Clayton DH, Bush SE, Johnson KP (2004) Ecology of congruence: past meets present. *Systematic Biology*, **53**, 165–173.

Clement M, Posada D, Crandall K (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, **9**, 1657–1660.

Corbet GB (1956) The life-history and host-relations of a hippoboscid fly *Ornithomyia fringillina* Curtis. *Journal of Animal Ecology*, **25**, 403–420.

Criscione CD, Blouin MS (2004) Life cycles shape parasite evolution: comparative population genetics of salmon trematodes. *Evolution*, **58**, 198–202.

Criscione CD, Blouin MS (2006) Parasite phylogeographic congruence with salmon host evolutionary significant units: implications for salmon conservation. *Molecular Ecology*, **16**, 993–1005.

Criscione CD, Cooper B, Blouin MS (2006) Parasite genotypes identify source populations of migratory fish more accurately than fish genotypes. *Ecology*, **87**, 823–828.

Criscione CD, Poulin R, Blouin MS (2005) Molecular ecology of parasites: elucidating ecological and microevolutionary processes. *Molecular Ecology*, **14**, 2247–2257.

Cruickshank RH, Johnson KP, Smith VS *et al*. (2001) Phylogenetic analysis of partial sequences of elongation factor 1α identifies major groups of lice (Insecta: Phthiraptera). *Molecular Phylogenetics and Evolution*, **19**, 202–215.

Cunningham CW, Collins TM (1994) Developing model systems for molecular biogeography: vicariance and interchange in marine invertebrates. In: *Molecular Ecology and Evolution: Approaches and Applications* (eds Schierwater B, Streit B, Wagner GP, De Salle R), pp. 405–434. Birkhauser-Verlag, Basel, Switzerland.

Darwin CR (1859) *On the Origin of Species by Means of Natural Selection*. John Murray, London.

Dybdahl MF, Lively CM (1996) The geography of coevolution: comparative population structures for a snail and its trematode parasite. *Evolution*, **50**, 2264–2275.

Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics*, **131**, 479–491.

Finston TL, Peck SB (1997) Genetic differentiation and speciation in *Stomion* (Coleoptera: Tenebrionidae): flightless beetles of the Galápagos Islands. *Biological Journal of the Linnean Society*, **61**, 183–200.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, **3**, 294–299.

Fuller MR, Seegar WS, Schueck LS (1998) Routes and travel rates of migrating Peregrine Falcons *Falco peregrinus* and Swainson's hawks *Buteo swainsoni* in the Western Hemisphere. *Journal of Avian Biology*, **29**, 433–440.

Funk DJ, Helbing L, Wernegreen JJ, Moran NA (2000) Intraspecific phylogenetic congruence among multiple symbiont genomes. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **267**, 2517–2521.

Gandon S, Capowiez Y, DuBois Y, Michalakis Y, Olivieri I (1996) Local adaptation and gene-for-gene coevolution in a metapopulation model. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **263**, 1003–1009.

Gatenbein B, Gatenbein-Ritter IA, Balloux F (2005) Evidence for recombination in scorpion mitochondrial DNA (Scorpiones: Buthidae). *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **272**, 697–704.

Gilbert DA, Lehman N, OíBrien SJ, Wayne RK (1990) Genetic fingerprinting reflects population differentiation in the California Channel Island fox. *Nature*, **344**, 764–767.

Giraud T (2006) Speciation in parasites: host switching does not automatically lead to allopatry. *Trends in Parasitology*, **22**, 151–152.

Gooding RH, Krafsur ES (2005) Tsetse genetics: contributions to biology, systematics, and control of tsetse flies. *Annual Review of Entomology*, **50**, 101–123.

Grant PR, Grant BR (2006) Evolution of character displacement in Darwin's Finches. *Science*, **313**, 224–226.

Grant PR, Grant BR, Smith JNM, Abbott IJ, Abbott LK (1976) Darwin's finches: population variation and natural selection. *Proceedings of the National Academy of Sciences, USA*, **73**, 257–261.

Hafner MS, Demastes JW, Spradling TA, Reed DL (2003) Cophylogeny between pocket gophers and chewing lice. In: *Tangled Trees: Phylogeny, Cospeciation and Coevolution* (eds Page RDM), pp. 195–220. University of Chicago Press, Illinois.

Hafner MS, Sudman PD, Villablanca FX *et al*. (1994) Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science*, **265**, 1087–1090.

Hoberg EP, Brooks DR, Siegel-Causey D (1997) Host–parasite cospeciation: history, principles and prospects. In: *Host–Parasite Evolution: General Principles and Avian Models* (eds Clayton DH, Moore J), pp. 212–235. Oxford University Press, Oxford, UK.

Hofkin BV, Wright A, Altenback J *et al*. (2003) Ancient DNA gives green light to Galápagos Land Iguana repatriation. *Conservation Genetics*, **4**, 105–108.

Huyse T, Poulin R, Théron A (2005) Speciation in parasites: a population genetics approach. *Trends in Parasitology*, **21**, 469–475.

Johnson KP, Williams BL, Drown DM, Adams RJ, Clayton DH (2002) The population genetics of host specificity: genetic differentiation in dove lice (Insecta: Phthiraptera). *Molecular Ecology*, **11**, 25–38.

Johnson KP, Yoshizawa K, Smith VS (2004) Multiple origins of parasitism in lice. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **271**, 1771–1776.

Kaliszewska ZA, Seger J, Rowntree VJ *et al*. (2005) Population histories of right whales (Cetacea: *Eubalaena*) inferred from mitochondrial sequence diversities and divergences of their whale lice (Amphipoda: *Cyamus*). *Molecular Ecology*, **4**, 3439–3456.

Kizirian D, Trager A, Donnelly MA, Wright JW (2004) Evolution of Galápagos Island Lava Lizards (Iguania: Tropiduridae: *Microlophlus*). *Molecular Phylogenetics and Evolution*, **32**, 761–769.

Krafsur ES (2002) Population structure of the tsetse fly *Glossina pallidipes* estimated by allozyme, microsatellite and mitochondrial gene diversities. *Insect Molecular Biology*, **11**, 37–45.

Krebs CJ (1989) *Ecological Methodology*, Harper Collins, New York, NY.

Lea W, Pak DK, Belanger CL, Spero HJ, Hall MA, Shackleton NJ (2006) Paleoclimate history of Galápagos surface waters over the last 135 000 yr. *Quaternary Science Reviews*, **25**, 1152–1167.

Leo NP, Hughes JM, Yang X *et al*. (2005) The head and body lice of humans are genetically distinct (Insecta: Phthiraptera, Pediculidae): evidence from double infestations. *Journal of Heredity*, **95**, 34–40.

Lively CM (1999) Migration, virulence, and the geographic mosaic of adaptation by parasites. *American Naturalist*, **153**, S34–S47.

Lymbery AJ, Dadour IR (1999) Genetic structure of the *Bovicola ovis* (Mallophaga: Trichodectidae) in Southwestern Australia. *Environmental Entomology*, **28**, 675–680.

Maa TC (1963) Genera and species of Hippoboscidae (Diptera): Types, synonomy, habitats and natural groupings. *Pacific Insects Monographs*, **6**, 1–186.

Maa TC (1969) A revised checklist and concise host index of Hippoboscidae (Diptera). *Pacific Insects Monographs*, **20**, 261–299.

Mantel N (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research*, **27**, 209–220.

Marshall AG (1981) *The Ecology of Ectoparasitic Insects*. Academic Press, London, UK.

McCoy KD, Boulinier T, Tirard C (2005) Comparative host-parasite population structures: disentangling prospecting and dispersal in the black-legged kittiwake *Rissa tridactyla*. *Molecular Ecology*, **14**, 2825–2838.

McCoy KD, Boulinier T, Tirard C, Michalakis Y (2003) Host-dependent genetic structure of parasite populations: differential dispersal of seabird tick host races. *Evolution*, **57**, 288–296.

Morgan AD, Gandon S, Bucking A (2005) The effect of migration on local adaptation in a coevolving system. *Nature*, **437**, 253–256.

Mulvey M, Aho JM, Lydeard CM, Leberg PL, Smith MH (1991) Comparative population genetic structure of a parasite (*Fascioloides magna*) and its definitive host. *Evolution*, **45**, 1628–1640.

Nadler SA (1995) Microevolution and the genetic structure of parasite populations. *Journal of Parasitology*, **81**, 395–403.

Nadler SA, Hafner MS, Hafner JC, Hafner DJ (1990) Genetic differentiation among chewing louse populations (Mallophaga: Trichodectidae) in a pocket gopher contact zone (Rodentia: Geomyidae). *Evolution*, **44**, 942–951.

Nieberding C, Morand S, Libois R, Michaux JR (2004) A parasite reveals cryptic phylogeographic history of its host. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **271**, 2559–2568.

Nieberding C, Morand S, Libois R, Michaux JR (2006) Parasites and the island syndrome: the colonization of the western Mediterranean islands by *Heligmnosomoides polygyrus* (Dujardin, 1845). *Journal of Biogeography*, **7**, 1212–1222.

Nieberding C, Olivieri I (2007) Parasites: proxies for host genealogy and ecology? *Trends in Ecology &Evolution*, **22**, 156–165.

Nielsen R, Wakeley J (2001) Distinguishing migration from isolation: a Markov chain Monte Carlo approach. *Genetics*, **158**, 885–896.

Page RDM (2003) Introduction. In: *Tangled Trees: Phylogeny, Cospeciation and Coevolution* (ed. Page RDM), pp. 1–21. University Chicago Press, Chicago, IL.

Page RD, Lee PL, Becher SA, Griffiths R, Clayton DH (1998) A different tempo of mitochondrial DNA evolution in birds and their parasitic lice. *Molecular Phylogenetics and Evolution*, **9**, 276–293.

Parent CE, Crespi BJ (2006) Sequential colonization and diversification of Galápagos endemic land snail genus *Bulimulus* (Gastropoda, Sylommatophora). *Evolution*, **60**, 2311–2328.

Perkins SL (2001) Phylogeography of Caribbean lizard malaria: tracing the history of vector borne parasites. *Journal of Evolutionary Biology*, **14**, 34–45.

Poulin R (2006) *Evolutionary Ecology of Parasites*. Princeton University Press, Princeton, New Jersey.

Price PW (1980) *Evolutionary Biology of Parasites*. Princeton University Press, Princeton, New Jersey.

Price RD, Beer JR (1963) Species of *Colpocephalum* (Mallophaga: Menoponidae) parasitic upon the Falconiformes. *Canadian Entomologist*, **95**, 731–763.

Price RD, Hellenthal RA, Palma RL (2003) World checklist of chewing lice with host associations and keys to families and genera. In: *The Chewing Lice: World Checklist and Biology Overview* (eds Price RD, Hellenthal RA, Palma RL, Johnson KP, Clayton DH), pp. 1–448. Illinois Natural History Survey Special Publication 24.

Rambaut A (1996) SE-AL: *Sequence Alignment Editor*.

Rannala B, Michalakis Y (2003) Population genetics and cospeciation: from processes to pattern. In: *Tangled Trees: Phylogeny, Cospeciation and Coevolution* (ed. Page RDM), pp. 120–143. University of Chicago Press, Chicago, Illinois.

Raufaste N, Rousset F (2001) Are partial Mantel tests adequate? *Evolution*, **55**, 1703–1705.

Reiczigel J, Rózsa L (2001) *Quantitative Parasitology 3.0.*, Budapest, Hungary.

Rice WR (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.

Rousset F (1997) Genetic differentiation and estimation of gene flow from *F*-statistics under isolation by distance. *Genetics*, **145**, 1219–1228.

Rozas J, Rozas R (1999) DNASP version 3: an integrated program for molecular population genetics and molecular evolution analysis. *Bioinformatics*, **15**, 174–175.

Schneider S, Doessli D, Excoffier L (2000) ARLEQUIN: *A Software for Population Genetic Data*. Genetics and Biometry Laboratory University of Geneva, Geneva, Switzerland .

Simon C, Frati F, Beckenbach A *et al*. (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, **87**, 651–704.

Smith CI, Farrell BD (2005) Phylogeography of the longhorn cactus beetle moneilema appressum LeConte (coleoptera: cerambycidae): was the differentiation of the Madrean sky-islands driven by Pleistocene climate changes? *Molecular Ecology*, **14**, 3049–3065.

Sorenson MD, Ast JC, Dimcheff DE, Yuri T, Mindell DP (1999) Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. *Molecular Phylogenetics and Evolution*, **12**, 105–114.

Steeves TE, Anderson DJ, Friesen VL (2005) A role for nonphysical barriers to gene flow in the diversification of a highly vagile seabird, the masked booby (*Sula dactylatra*). *Molecular Ecology*, **14**, 3877–3887.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, **25**, 4876–4882.

Tye A, Snell HL, Peck SB, Adserson H (2002) Outstanding terrestrial features of the Galapagos archipelago. In: *A Biodiversity Vision for the Galapagos Islands* (ed. Bensted-Smith R), pp. 12–23. Charles Darwin Foundation and World Wildlife Fund, Puerto Ayora, Galapagos, Ecuador.

Wakeley J (2000) The effects of subdivision on the genetic divergence of populations and species. *Evolution*, **54**, 1092–1101.

de Vries T (1975) The breeding biology of the Galapagos Hawk, *Buteo galapagoensis*. *Le Gerfaut*, **65**, 29–57.

Wares JP (2002) Community genetics in the northwestern Atlantic intertidal. *Molecular Ecology*, **11**, 1131–1144.

Whiteman NK, Matson KD, Bollmer JL, Parker PG (2006a) Disease ecology in the Galápagos hawk (*Buteo galapagoensis*): Host genetic diversity, parasite load and natural antibodies. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **273**, 797–804.

Whiteman NKS, ·nchez P, Merkel J, Klompen H, Parker PG (2006b) Cryptic host specificity of an avian skin mite (Epidermoptidae) vectored by louseflies (Hippoboscidae) associated with two endemic Galápagos bird species. *Journal of Parasitology*, **92**, 1218–1228.

Whiteman NK, Parker PG (2004a) Effects of host sociality on ectoparasite population biology. *Journal of Parasitology*, **90**, 939–947.

Whiteman NK, Parker PG (2004b) Body condition and parasite load predict territory ownership in the Galapagos Hawk. *Condor*, **106**, 616–622.

Whiteman NK, Parker PG (2005) Using parasites to infer host population history: a new rationale for parasite conservation. *Animal Conservation*, **8**, 175–181.

Whiteman NK, Santiago-Alarcon D, Johnson KP, Parker PG (2004) Differences in straggling rates between two genera of dove lice (Insecta: Phthiraptera) reinforce population genetic and cophylogenetic patterns. *International Journal for Parasitology*, **34**, 1113–1119.

Wright S (1951) The genetical structure of populations. *Annals of Eugenics*, **15**, 323–354.

Yoshizawa K, Johnson KP (2003) Phylogenetic position of Phthiraptera (Insecta: Paraneoptera) and elevated rate of evolution in mitochondrial 12S and 16S rDNA. *Molecular Phylogenetics and Evolution*, **29**, 102–114.

This study arose out of Noah K. Whiteman's PhD dissertation, supervised by Patricia G. Parker in the Department of Biology at the University of Missouri-St Louis, and through a collaboration with Rebecca T. Kimball in the Department of Zoology at the University of Florida-Gainesville. Noah's interests are in conservation biology, the biology of co-evolved systems, and disease ecology. He is currently a postdoctoral fellow in the Department of Organismic and Evolutionary Biology at Harvard University. Patricia G. Parker is currently the E. Desmond Lee Professor of Zoological Studies at the University of Missouri-St Louis and Saint Louis Zoo. Her research program spans behavioural ecology, conservation biology and disease ecology and focuses on the avifauna of the Galápagos Islands, Ecuador. Rebecca T. Kimball is currently Associate Professor in the Department of Zoology at the University of Florida. Her research interests include behavioural ecology and evolutionary genetics, mostly of birds.

Supplementary material

The following Supplementary material is available for this article:

Fig. S1 Video clip showing the highly mobile amblyceran louse *Colpocephalum turbinatum* running across the wing feathers of a Galápagos hawk (*Buteo galapagoensis*).

Table S1 Pairwise comparisons of interisland genetic differentiation in the louse *Degeeriella regalis*.

Table S2 Pairwise comparisons of interisland genetic differentiation in the louse *Colpocephalum turbinatum*.

Table S3 Pairwise comparisons of interisland genetic differentiation in the lousefly *Icosta nigra*.

Table S4 MDIV estimates of the nonequilibrium migration rates and estimates of the divergence between population pairs of *Buteo galapagoensis*.

Table S5 MDIV estimates of the nonequilibrium migration rates and estimates of the divergence times between population pairs of *Degeeriella regalis*.

Table S6 MDIV estimates of the nonequilibrium migration rates and estimates of the divergence times between population pairs of *Colpocephalum turbinatum*.

Table S7 MDIV estimates of the nonequilibrium migration rates and estimates of the divergence times between population pairs of *Icosta nigra*.

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