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Phoretic dispersal influences parasite population genetic structure

Emily DiBlasi[1] | Kevin P. Johnson[2] | Sydney A. Stringham[1] | Angela N. Hansen[1] | Andrew B. Beach[1] | Dale H. Clayton[1] | Sarah E. Bush[1]

[1]Department of Biology, University of Utah, Salt Lake City, Utah

[2]Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, Champaign, Illinois

Correspondence
Emily DiBlasi, Department of Biology, University of Utah, Salt Lake City, UT.
Email: diblasi.emily@gmail.com

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Abstract

Dispersal is a fundamental component of the life history of most species. Dispersal influences fitness, population dynamics, gene flow, genetic drift and population genetic structure. Even small differences in dispersal can alter ecological interactions and trigger an evolutionary cascade. Linking such ecological processes with evolutionary patterns is difficult, but can be carried out in the proper comparative context. Here, we investigate how differences in phoretic dispersal influence the population genetic structure of two different parasites of the same host species. We focus on two species of host-specific feather lice (Phthiraptera: Ischnocera) that co-occur on feral rock pigeons (*Columba livia*). Although these lice are ecologically very similar, "wing lice" (*Columbicola columbae*) disperse phoretically by "hitchhiking" on pigeon flies (Diptera: Hippoboscidae), while "body lice" (*Campanulotes compar*) do not. Differences in the phoretic dispersal of these species are thought to underlie observed differences in host specificity, as well as the degree of host–parasite cospeciation. These ecological and macroevolutionary patterns suggest that body lice should exhibit more genetic differentiation than wing lice. We tested this prediction among lice on individual birds and among lice on birds from three pigeon flocks. We found higher levels of genetic differentiation in body lice compared to wing lice at two spatial scales. Our results indicate that differences in phoretic dispersal can explain microevolutionary differences in population genetic structure and are consistent with macroevolutionary differences in the degree of host–parasite cospeciation.

KEYWORDS
birds, community ecology, host–parasite interactions, insects, population genetics—empirical, species interactions

1 | INTRODUCTION

Dispersal, or the movement of individuals away from their birthplace, is central in shaping ecological and evolutionary processes (Clobert, Baguette, Benton, & Bullock, 2012). Dispersal has a variety of adaptive functions, including exploitation of resource-rich habitats, avoidance of inbreeding and mitigation of intra- and inter-specific competition (Clobert et al., 2012; Edelaar & Bolnick, 2012; Ronce, 2007). Dispersal influences individual fitness and population dynamics, as well as gene flow, random genetic drift and population genetic structure. It has important effects at the community level, arranging individuals and species into new interactions and altering selective regimes and fitness landscapes. Acting together, selection and dispersal provide much of the ecological context for codiversification of

interacting groups (Althoff, Segraves, & Johnson, 2014; Clayton, Bush, & Johnson, 2015).

Dispersal allows organisms to specialize on patchily distributed resources (MacArthur & Pianka, 1966), whether the patches are islands, ponds or host plants and animals (Blasco-Costa & Poulin, 2013; Koop, DeMatteo, Parker, & Whiteman, 2014). These patches may be resource-rich, but dispersing among ephemeral, spatially isolated patches can be risky and difficult. Risks include failing to find suitable habitat or failing to find suitable mates. These risks are exacerbated among small, relatively immobile organisms, such as wingless insects, mites and worms. Some animals have solved this dispersal problem by hitching rides on more mobile organisms. This behaviour is called "phoresy" (Farish & Axtell, 1971; Houck & O'Connor, 1991).

Phoresy is an ancient and widespread behaviour. Phoretic associations are known from amber and fossil specimens, with the oldest known case being a 320-million-year-old mite attached to the thorax of an orthopteran insect (Robin et al., 2016). Phoretic dispersal is known to occur among hundreds of species of insects, arachnids, crustaceans, millipedes, annelids, nematodes, molluscs, echinoderms and rotifers (Clausen, 1976; Colwell, 1985; Darwin 1882; Fronhofer et al., 2013; Heyneman, Colwell, Naeem, Dobkin, & Hallet, 1991; Houck & O'Connor, 1991; Keirans, 1975; Lopez, Rodrigues, & Rios, 1999; Lee et al., 2017). Phoresis may have evolved as an adaptive response to competition. For example, flower mites (*Spadiseius calyptrogynae*) engage in density-dependent phoretic dispersal (Fronhofer et al., 2013), and the pseudoscorpion (*Paratemnoides nidificator*) is most likely to attempt phoresy when there are many pseudoscorpions living together in a single colony (Tizo-Pedroso & Del-Claro, 2007). Competition–colonization trade-offs such as these are well known in plants, but are poorly studied in other communities (Livingston et al., 2012).

Despite the pervasiveness of phoresis throughout the animal kingdom, the influence of phoretic dispersal on population genetic structure is poorly understood. Here, we investigate the influence of phoretic dispersal on population genetic structure by comparing two parasite species from the same host species, one which uses phoresis and one which does not. We focus on the particularly tractable host–parasite system of two species of host-specific feather lice (Insecta: Phthiraptera: Ischnocera) that parasitize feral rock pigeons (*Columba livia*). "Wing lice" (*Columbicola columbae*) and "body lice" (*Campanulotes compar*) are both obligate, permanent, parasites that pass all stages of their life cycle on the feathers of birds. Although wing and body lice are distantly related, they are so ecologically similar to each other that they are often considered "ecological replicates" (Clayton et al., 2015). Both wing and body lice glue their eggs to the feathers with a glandular cement. Upon hatching, neither the immatures (three nymphal instars) nor the adults leave the body of the host under their own power as their appendages are highly specialized for locomotion on feathers (Bartlow, Villa, Thompson, & Bush, 2016). Indeed, feather lice do not even venture onto the skin of the host (Clayton et al., 2015). Dispersal of wing and body lice takes place mainly during periods of direct contact between feathers of parents and their offspring in the nest, or contact between feathers of mated individuals (Harbison, Bush, Malenke, & Clayton, 2008).

Although there are many similarities between wing and body lice, they primarily differ in one mode of dispersal. Wing lice are capable of dispersing phoretically on pigeon flies (Diptera: Hippoboscidae), but body lice are not (Figure 1). Experiments with captive birds have shown that wing lice attach to pigeon flies (*Pseudolynchia canariensis*) and disperse to new host individuals in sufficient numbers to establish new populations (Harbison & Clayton, 2011; Harbison, Jacobsen, & Clayton, 2009). As in other systems, phoresis may facilitate a competition–colonization trade-off between coinfesting parasites. Experiments with these lice have shown that body lice are competitively superior to wing lice. When body lice are present, wing louse populations are smaller and wing lice shift their position on the host to microhabitats where body lice are less common (Bush & Malenke, 2008). Wing lice may use phoretic dispersal to escape from birds with body lice and then colonize birds without body lice (Harbison et al., 2008).

Phoresis appears to be linked to emergent patterns of community structure in this system. Hippoboscid flies, the phoretic vectors of wing lice, can easily move between different host species. This provides opportunities for wing lice to disperse among more host individuals and across greater geographic distances than body lice (Harbison & Clayton, 2011). Johnson, Williams, Drown, Adams, and Clayton (2002) examined the host and geographic specificity of several species of wing lice (*Columbicola* spp.) and body lice (*Physconelloides spp.*) that co-occur on New World doves. Using mitochondrial

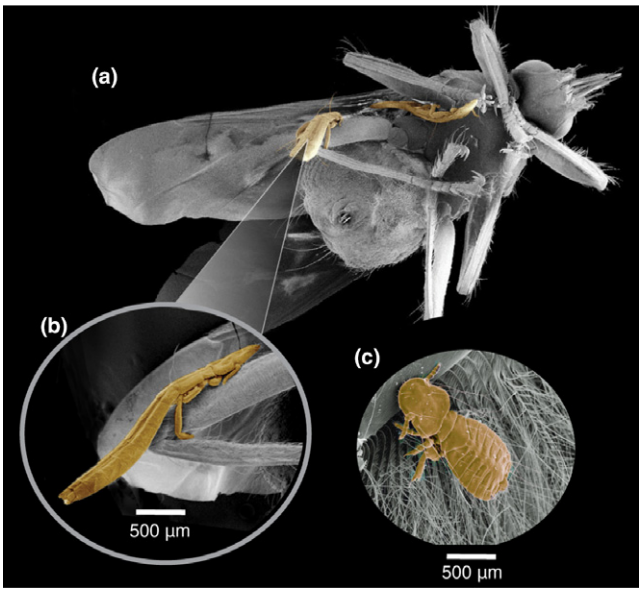

FIGURE 1 (a) False coloured SEM of phoretic wing lice (*Columbicola columbae*) attached to the legs of a pigeon fly (*Pseudolynchia canariensis*); (b) enlarged view showing how the wing louse uses its third pair of legs to grasp the fly's leg (modified from Harbison & Clayton, 2011); (c) body lice (*Campanulotes compar*) do not engage in phoresis with flies, in part, because of their shorter legs

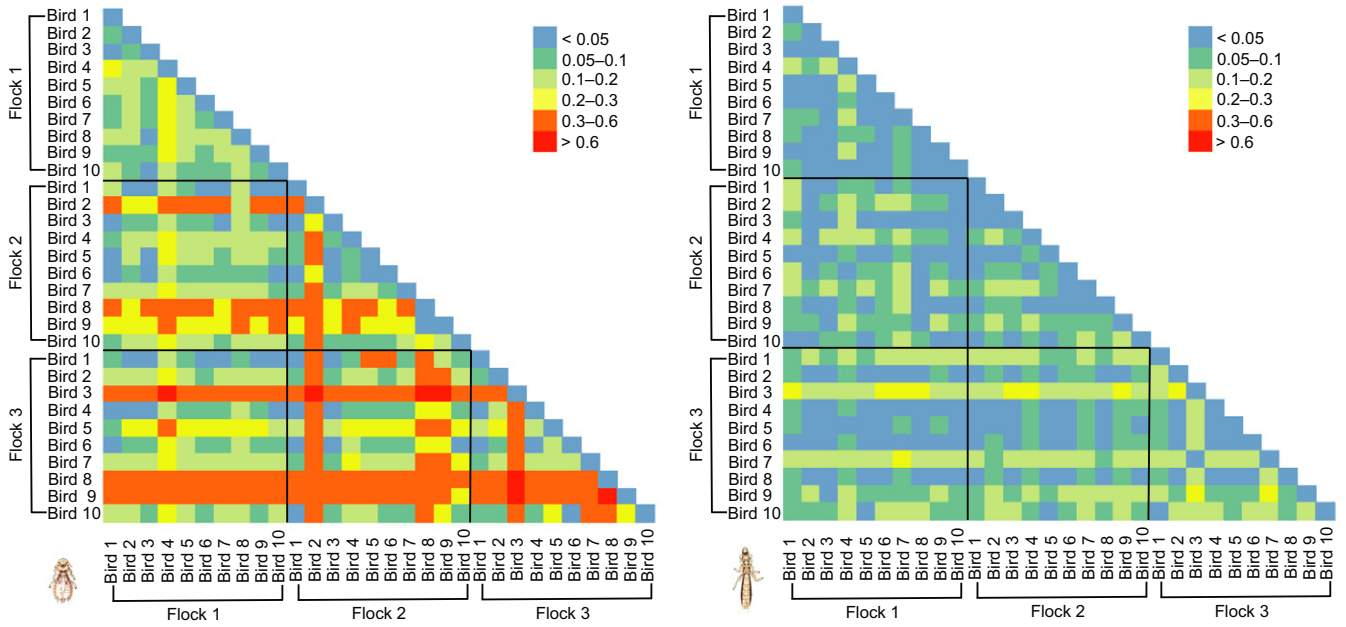

FIGURE 2 Matrix of pairwise F_{ST} values between genotypes of body lice subpopulations (left) and wing lice subpopulations (right) from the same birds. Warm colours indicate greater genetic differentiation than cool colours. Flock numbers correspond to site numbers in Figures 3 and 4

data (COI) to identify distinct louse haplotypes, Johnson et al. (2002) found that species of wing lice occur on more host species and across wider geographic ranges than body lice. In other words, body lice were more host-specific and more geographically specific than wing lice. Moreover, studies comparing host and parasite phylogenies showed that body lice also exhibit more cophylogenetic congruence, and a more pronounced history of host–parasite cospeciation, than wing lice (Clayton & Johnson, 2003). Differences in phoretic dispersal are often invoked to explain these differences. However, a comparative study of population structure at a finer scale, such as among host flocks and among host individuals, is needed to fully understand the role of phoretic dispersal differences in shaping micro- and macroevolutionary patterns. Here, we compare the population genetic structure of a single wing louse species (*Columbicola columbae*) and a single body louse species (*Campanulotes compar*). In the New World, these species of lice are only found on a single host species, the rock pigeon (*Columba* livia). Thus, this system is quite tractable; moreover, differences in the dispersal of wing and body lice have already been rigorously quantified in laboratory and field experiments (Harbison & Clayton, 2011; Harbison et al., 2009).

Here, we tested the hypothesis that wing lice have less genetic structure than body lice at the population level. We tested this hypothesis by comparing the population genetic structure of rock pigeons, wing lice and body lice across several spatial scales. As population genetic analyses are strongly impacted by sampling design (Meirmans, 2015; Papadopoulou & Knowles, 2016), we used a hierarchical study design in which we sampled rock pigeons and their wing and body lice among three sites in Salt Lake City, Utah. We compared genetic variation within each of the two species of lice across two spatial scales: (a) genetic variation of lice among individual birds within a single pigeon flock and (b) genetic variation of lice among three pigeon flocks. We also investigated whether other factors, such as different forms of dispersal and population size, influence the population differentiation of wing lice versus body lice.

2 | METHODS

2.1 | Field work

All work was approved by the University of Utah Institutional Animal Care and Use Committee (protocol #11-07018). We used walk-in traps to obtain live pigeons at three sites, each with a large bridge that was home to at least 100 pigeons (Supporting information: Figure S1). The three sites were separated by at least 7 km from one another. Birds were trapped consecutively in June 2014 and June 2015. Once trapped, pigeons were brought back to the laboratory, where their lice were killed by ethyl acetate fumigation in a chamber for 15 min, followed by gentle ruffling to dislodge the lice (Villa, Goodman, Ruff, & Clayton, 2016). Lice were counted and preserved in 95% ethanol for subsequent DNA extraction. We ultimately compared the genetics of lice from the first 10 birds from each bridge coinfested with at least 10 wing lice and 10 body lice. In total, we extracted DNA from 10 wing lice and 10 body lice from each of 10 birds from three bridges, for a total of 30 birds. A blood sample (~10 μl) was taken from each of the 30 birds using a sterile 27-gauge needle to puncture the brachial vein, followed by collection of blood in a heparinized microheamatocrit tube. The blood samples were later used to extract DNA from the birds. Birds were released back at the bridge where they had been captured after fitting them

with a numbered aluminium band and a single coloured plastic band (different colours for the different bridges). The bridges were visited several more times over the course of a year to observe and, in some cases, re-trap birds for identification. None of the birds were observed to disperse between the three bridges; that is, no bird with the "wrong" colour band was ever observed or trapped at a bridge. If birds were recaptured, their parasites were removed but these re-examined birds are not used in this study.

2.2 | Population genetic analyses

The 10 wing lice and 10 body lice collected from each bird were genotyped at each of 8 microsatellite loci developed for this study (Supporting information: Table S1). We developed 17 primer sets specific to wing lice (*Columbicola columbae*) and 13 primer sets specific to body lice (*Campanulotes compar*). Variable nuclear microsatellite loci were identified by searching for STR motifs (di, tri, tetra) with MSATCOMMANDER (Faircloth, 2008; Rozen & Skaletsky, 2000) in sequences generated by Illumina sequencing from 30 pooled individuals. Sequences used to search for microsatellite motifs had BLAST alignment scores ≥200, compared with the human body louse (*Pediculus humanus corporis*) genome, which is the only published louse genome (Kirkness et al., 2010). Each microsatellite locus was evaluated with a multistep screening process to ensure quality data as suggested by Selkoe and Toonen (2006) and Fernandez-Silva et al. (2013). This filtering yielded eight microsatellites specific to wing lice and eight microsatellites specific to body lice, which were appropriate for analyses. The 17 microsatellite loci used to genotype host pigeons were developed by Chun-Lee et al. (2007), Stringham et al. (2012), and Traxler, Brem, Muller, and Achmann (2000). DNA extractions of wing lice, body lice and pigeons were performed using the DNeasy Blood and Tissue kit (Qiagen). DNA was extracted from lice as described by Johnson (2001). Multiplex PCRs with a universal primer and fluorophore were used to genotype the samples (Blacket, Robin, Good, Lee, & Miller, 2012; Schuelke, 2000). The universal primer tail M13 (5′ CAC GAC GTT GTA AAA CGA C 3′) was added to the 5′ end of the locus-specific forward primer. M13 labelled primers were tagged with FAM, PET, NED, or VIC (Applied Biosystems). The two forward primers and the appropriate locus-specific reverse primer were used in PCRs. An ABI 3100 Genetic Analyzer (Applied Biosystems) was used to resolve PCR products and was run with the 500 LIZ size standard. GENEMAPPER v 3.7 (Applied Biosystems) was used to determine allele sizes.

Lice were genotyped from 10 host individuals at each of the three sites for a total of 300 wing lice and 300 body lice. The 30 host birds were also genotyped at 17 microsatellite loci. We use the term "subpopulation" to refer to conspecific lice living on a single host individual. We use "population" to refer to conspecific lice across all 10 birds from a single flock. We use the term "metapopulation" to refer to conspecific lice across all 30 birds (from three sites/flocks).

Genotyping error and null allele frequencies were estimated with Micro-checker (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). Linkage disequilibrium and deviations from Hardy–Weinberg equilibrium for each marker within wing lice and within body lice were assessed with Genepop (Raymond & Rousset, 1995). The descriptive statistics, the number of alleles observed (N_A), observed heterozygosity (H_O) and expected heterozygosity (H_S), were calculated using GENODIVE (v 2.0; Meirmans & Van Tienderen, 2004). The inbreeding coefficient (F_{IS}) and 95% confidence intervals (CIs) were calculated by bootstrapping (10,000 iterations) and calculated in the R (v 3.3.3) package "DIVERSITY" (Keenan, McGinnity, Cross, Crozier, & Prodohl, 2013; R Core Team 2016). We compared subpopulation H_S to subpopulation size for each louse species using a logistic regression with a binomial distribution and logit link in JMP (v 13.2.1).

To compare genetic differentiation between louse subpopulations, pairwise F_{ST} values were calculated in ARLEQUIN (v 3.5) and significance was tested with 10,000 permutations (Excoffier, Laval, & Schneider, 2005). Critical significance levels were computed with corrections for false discovery rates to control for multiple comparisons (Benjamini & Hochberg, 1995). Global F_{ST} values and 95% confidence intervals (CIs) were calculated by bootstrapping across louse individuals (10,000 iterations) with DIVERSITY. For polymorphic microsatellite loci, empirical maximum values of F_{ST} are often lower than the theoretical maximum of 1 (Hedrick, 2005; Jost, 2008). Therefore, multiple differentiation statistics and estimators were calculated and compared.

Louse genetic variation was also partitioned into two biologically relevant levels: (a) among host individuals within a single pigeon flock and (b) among host flocks. All of the conspecific lice genotyped from a single bird (10 wing lice and 10 body lice) were treated as an a priori defined population. To assess whether there was significant population structure of wing and body lice at each level, we performed an analysis of molecular variance (AMOVA) in ARLEQUIN.

To test for an association between genetic and geographic distance matrices for each louse species, Mantel tests with 10,000 permutations were used (Mantel, 1967). The pairwise geographic and genetic distance matrices used in the Mantel tests were calculated in GENODIVE. Geographic distances were taken from coordinates at the centre of each of the three distinct flock sites. Genetic distance matrices of pairwise F_{ST} values were transformed to $F_{ST}/(1 - F_{ST})$. In addition, partial-Mantel tests corrected for geographic distance were implemented in GENODIVE with 10,000 permutations to compare genetic distance matrices of pairwise F_{ST} values of each species of louse to genetic distance matrices of pairwise F_{ST} values of the pigeon host from which they were collected.

2.3 | Multivariate analyses

To identify the optimal number of genetic clusters in the data without predefining populations, we used the *find.clusters()* function implemented in the R package "ADEGENET" (Jombart & Ahmed, 2011). The optimal number of genetic clusters was chosen for each species by selecting the lowest Bayesian information criterion (BIC) values. For wing and body lice, we tested values of $k = 1$–30 corresponding to the 30 subpopulations of each louse species, with multiple runs at

each value of *k*. For pigeons, we tested values of $k = 1$–3 corresponding to the three flock sites, with multiple runs at each value of *k*. Using the groupings from *k*-means clustering, we used the *dapc* function to describe the genetic clusters with the discriminant analysis of principal components (DAPC; Jombart, Devillard, & Balloux, 2010). Ordination plots were used to visualize the DAPC analysis, with axes representing the first two principal components of the DAPC. For each analysis, principal components were retained accounting for at least 84% of the total variance in the data. In additional analyses, louse populations were also predefined by the flock site from which they were collected. When louse genotypes were grouped by flock, two discriminant functions were retained.

2.4 | Modelling private versus shared alleles

We compared the allele frequencies of the two different louse species using microsatellite markers. To directly compare the degree of genetic differentiation between wing and body lice, we used generalized linear mixed-effects models (GLMM) with a binomial distribution and logit link. We predicted private alleles within each species across sampling sites by modelling the fixed effects of the ratio of private to shared alleles in each louse species, with sampling site included as a random effect. The model had 48 observations from three sites, and the model intercept was set as the ratio of private to shared alleles for body lice. We also predicted private alleles within each species across host sampled by modelling the fixed effects of the ratio of private to shared alleles in each louse species, and with host included as a random effect. The model had 480 observations from 30 hosts, and the model intercept was set as the ratio of private to shared alleles for body lice. The "lme4" package in R was used to fit each GLMM (Bates, Machler, Bolker, & Walker, 2015).

3 | RESULTS

3.1 | Louse and pigeon population genetic patterns

Wing lice were more prevalent and abundant than body lice at all three sites (Supporting information: Table S2). We extracted DNA from 300 wing lice and 300 body lice. Three body lice were excluded because too little DNA was amplified from them. Microsatellites for each louse species showed no evidence of allelic dropout. Linkage disequilibrium was not significant among loci for either louse species. Neither wing nor body louse populations showed departures from Hardy–Weinberg equilibrium. The mean observed heterozygosity (H_o) was 0.449 for body lice and 0.557 for wing lice (Supporting information: Table S3). Subpopulation heterozygosity did not correlate with subpopulation size for either species of louse (logistic regression body lice $n = 30$, $p = 0.8570$; wing lice $n = 30$, $p = 0.7941$). A weak yet significant pattern of isolation by distance was found for body lice (Mantel $r = 0.061$, $p = 0.015$), while a marginally nonsignificant correlation was found between genetic and geographic distances for wing lice (Mantel $r = 0.062$, $p = 0.060$). Thirty pigeons were genotyped. Indices of genetic diversity are reported in Supporting information: Table S4. The hierarchical AMOVA (Table 1) indicates that pigeons had low, yet significant, genetic differentiation among the three flocks (F_{ST} 0.012, $p < 0.0001$). Almost all of the genetic variance (98%) was accounted for by sampling within flocks. The ordination plot showing the first two principal components of the DAPC for the host genotypes show overlapping clusters (Supporting information: Figure S2). Pigeon population genetic structure did not correlate with louse population genetic structure for either louse species: body lice (partial-Mantel controlled for geographic distance, $r = 1.000$, $p = 0.584$; Mantel $r = -0.492$, $p = 0.492$); wing lice (partial-Mantel controlled for geographic distance, $r = 1.000$, $p = 0.581$; Mantel $r = 0.979$, $p = 0.328$).

3.2 | Wing versus body louse genetic structure

Both species of lice were significantly structured between birds in the same flock and between birds in different flocks (Table 1). Genetic differentiation between body louse subpopulations was larger than the differentiation seen between wing louse subpopulations in 83% (360/435) of all possible comparisons (Figure 2). Most body louse subpopulations were significantly structured. After correcting for false discovery rates, 92% (401/435) of pairwise F_{ST} values were significantly different from zero (Supporting information: Table S5). In contrast, only 61% (265/435) of pairwise F_{ST} values in wing lice were significantly different from zero (Supporting information: Table S6). G''_{ST} values followed the same pattern as F_{ST} values for both wing and body lice, yet the degree of differentiation was larger for G''_{ST} values (Supporting information: Table S7). Additionally, 23% of the total genetic variation in body lice was distributed among

TABLE 1 Analysis of molecular variation for body lice, wing lice and pigeons

Source of variation	% Variation	Fixation indices	*p* value
Body lice			
Among lice on individual birds	77.5	$F_{ST} = 0.225$	$p < 0.0001$
Among lice on different birds within a flock	21.2	$F_{SC} = 0.215$	$p < 0.001$
Among lice on different flocks of birds	1.4	$F_{CT} = 0.014$	$p < 0.05$
Wing lice			
Among lice on individual birds	92.5	$F_{ST} = 0.075$	$p < 0.0001$
Among lice on different birds within a flock	6.8	$F_{SC} = 0.069$	$p < 0.001$
Among lice on different flocks of birds	0.6	$F_{CT} = 0.006$	$p < 0.05$
Pigeons			
Within flocks	98.8	$F_{ST} = 0.012$	$p < 0.001$
Among flocks	1.2		

body louse subpopulations (F_{SC} 0.215, $p < 0.001$; Table 1) compared to only 8% among wing louse subpopulations (F_{SC} 0.069, $p < 0.001$).

The global F_{ST} value from a hierarchical AMOVA indicates that body lice are highly genetically differentiated among flocks (F_{ST} 0.225, $p < 0.0001$; Table 1), while wing lice are only moderately differentiated (F_{ST} 0.075, $p < 0.0001$). The 95% CIs of F_{ST} values did not overlap when compared either within or between flocks (Figure 3; Supporting information: Table S7). When body lice subpopulations were grouped by flock, the first two principal component axes of the DAPC separated the distributions of genetic clusters, indicating a high degree of genetic differentiation of body lice between the three flocks (Figure 4). In contrast, the first two principal component axes of the DAPC for wing lice revealed overlapping distributions of genetic clusters, indicating a lower degree of genetic differentiation between flocks (Figure 4). When lice subpopulations were grouped by host bird from which they were collected, the first two principal component axes of the DAPC separated three genetic clusters for body lice (Supporting information: Figure S3a), while all genetic clusters for wing lice were overlapping (Supporting information: Figure S3b), indicating a high degree of genetic differentiation of body lice between birds.

The *k*-means clustering algorithm displayed the lowest BIC values at 14 clusters for body lice and 10 clusters for wing lice. Body louse clusters 2, 3 and 13 show a large degree of separation from the other clusters (Supporting information: Figure S4a). Lice assigned membership to clusters 2, 3 and 13, corresponded to body louse subpopulations from Bird 3, Bird 8 and Bird 9 in Flock 3 (Supporting information: Table S8). In contrast, wing louse clusters 2 and 6 show a small degree of separation from the other clusters (Supporting information: Figure S4b). Wing lice assigned membership to clusters 2 and 6 parasitized birds at all three flock sites and thus do not correspond to separate subpopulations on individual birds (Supporting information: Table S9).

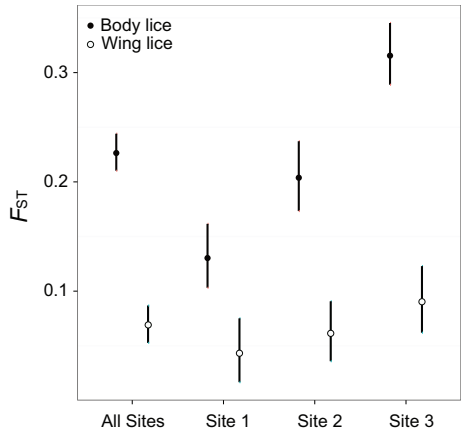

FIGURE 3 Global F_{ST} values for wing and body lice subpopulations at all sites and within each site. Bars on the graphs indicate 95% confidence intervals obtained from bootstrapping over individual louse genotypes

3.3 | Modelling private versus shared alleles

The ratio of private to shared alleles for wing lice was lower than that for body lice analysed with respect to site (GLMM; $Z = -6.012$; $p < 0.001$) or individual bird (GLMM; $Z = -8.808$; $p < 0.001$; Table 2). Specifically, the probability of finding a private allele in a flock was 1.9 times higher for body lice than for wing lice. The probability of finding a private allele on a bird was 3.4 times higher for body lice than for wing lice.

4 | DISCUSSION

When individuals disperse between populations and contribute to the gene pool, population genetic structure is reduced (Bohonak, 1999; Broquet & Petit, 2009). However, few empirical studies have directly assessed how particular modes of dispersal influence genetic structure. Here, we test how one particular mode of dispersal, phoresis, influences the population genetic differentiation of parasites. Our study takes a comparative approach and examines the population genetic structure of ecologically similar, yet distantly related parasites that differ in phoretic dispersal. We found that wing lice, which can disperse phoretically, have less population genetic structure among host individuals and among host populations than body lice, which are not phoretic.

Specifically, our results show that fly-mediated dispersal likely enhances gene flow and erodes population genetic structure in wing lice, compared to body lice. Differences in phoretic dispersal between wing and body lice are consistent with the observed differences in population genetic structure detected at two spatial scales in our study. Populations of nonphoretic body lice were more genetically differentiated than wing lice among individual birds (subpopulations) and among flocks (populations). Thus, phoresy provides an opportunity for wing lice to move independently of their hosts and influences microevolutionary patterns of diversification in these organisms.

Determinants of parasite population genetic structure are complex (Barrett, Thrall, Burdon, & Linde, 2008; Criscione, 2008; Maze-Guilmo, Blanchet, McCoy, & Loot, 2016), and it is possible that ecological factors other than phoresis may have also influenced genetic variation in this study. Previous experimental evidence has shown that the rate of horizontal dispersal of wing and body lice between pigeons that are in direct contact does not differ significantly (Harbison et al., 2008). However, vertical dispersal of wing lice from parents to offspring occurs at slightly higher rate than in body lice. If population structure were shaped mainly by dispersal of parasites from parents to offspring, we would expect that genetic distance matrices of the parasite and host would be correlated (Van Schaik, Kerth, Bruyndonckx, & Christe, 2014). In our study, genetic distances were not significantly correlated with the host for either louse species. Thus, there is no evidence that different rates of vertical dispersal cause the observed differences in population genetic structure of wing and body lice. However, only thirty hosts and a subset of their

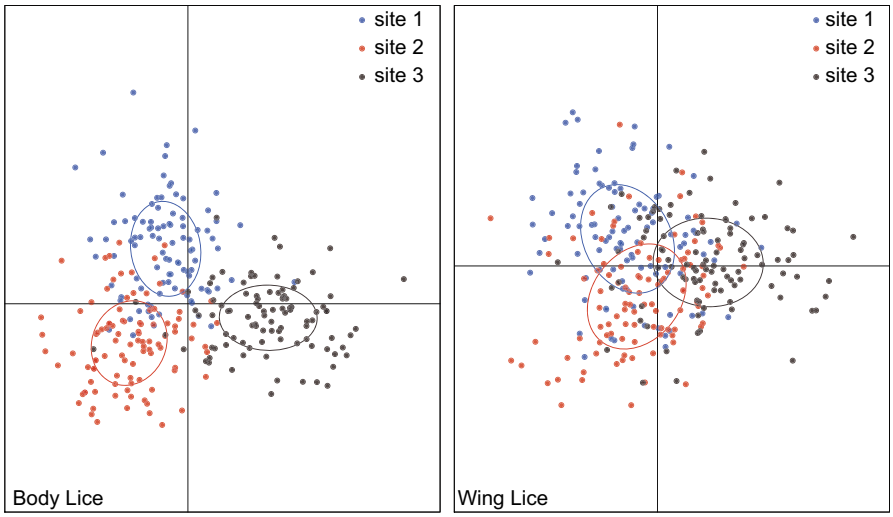

FIGURE 4 Ordination plots showing the first two principal components of the discriminant analysis of principal components (DAPC) for body lice (left) and wing lice (right). Colours show the sites from which lice were collected (Site 1: blue; Site 2: red; Site 3: grey). Each dot represents the genotype of an individual louse. Circles represent confidence intervals of the DAPC

TABLE 2 GLMM summary testing the probability that a given allele is (a) unique to the subpopulation (private allele) compared to all other lice at each collection site respective of species or (b) is a private allele for that louse subpopulation on its individual host bird

Random effects	Variance	Standard deviation			Random effects	Variance	Standard deviation		
(a)					(b)				
Site	1.15E−16	1.07E−08			Host	0.013	0.114		
Fixed effects	**Estimate**	**Standard error**	***Z*-value**	**Pr (>|z|)**	**Fixed effects**	**Estimate**	**Standard error**	***Z*-value**	**Pr (>|z|)**
Intercept (body lice)	−0.488	0.086	−5.65	<0.001*	Intercept (body lice)	−1.599	0.089	−17.91	<0.001*
Wing lice	−0.920	0.153	−6.01	<0.001*	Wing lice	−1.361	0.155	−8.81	<0.001*

Asterisks indicate statistical significance in probability tests.

wing and body louse subpopulations were genotyped in this study. For a more thorough examination of the effect of vertical dispersal on wing and body louse population structure, additional populations should be assessed.

Different evolutionary forces (drift, mutation and gene flow) interact over time and generate patterns of genetic differentiation (Marko & Hart, 2011). Population size influences the strength of genetic drift in populations. Thus, we recorded the subpopulation sizes of wing lice and body lice on each bird in our study. As body louse subpopulations were typically smaller in size than wing louse subpopulations, we would expect drift to play a greater role in shaping population genetic differentiation in body lice than wing lice. We found that genetic heterozygosity was not correlated with the subpopulation size of wing or body lice. However, this snapshot of the census population size of lice on pigeons may not accurately reflect long term population dynamics. It is possible that wing and body lice have different effective population sizes that could have contributed to the observed patterns of population differentiation.

Differences in host movement and sociality are also known to influence spatial distribution and population genetic structure of their parasites (Barrett et al., 2008; Harper, Spradling, Demastes, & Calhoun, 2015; Van Schaik et al., 2014). This may be one reason we did not find a significant pattern of isolation by distance (IBD) for wing and body louse populations. However, in our tests for IBD, we only had three geographic data points, one for each flock site. This limited spatial sampling may not be sufficient to detect a relationship between genetic and geographic distance, or perhaps IBD is more relevant at a larger geographic scale. We also found that the pigeon flocks in this study had a low yet significant amount of genetic structure among sites <10.5 km apart (Table 1). Although pigeons are known to occasionally move between sites (Johnston & Janiga, 1995), our data suggest that the pigeons in our study moved very little. However, in our study, both the wing lice and body lice from Bird 3 at Site 3 were substantially more genetically differentiated than other louse subpopulations. These data suggest that Bird 3 may be a recent immigrant, which could inflate our estimates of genetic differentiation among louse subpopulations. To address this issue, we also examined the population genetic structure of lice when subpopulations from Bird 3 are removed from the analyses (Supporting information: Figure S5). This did not change the pattern: body louse subpopulations were still more genetically differentiated when compared with wing lice.

Host sociality could also contribute to the observed patterns of parasite population genetic structure in this study. Only the most heavily coinfested hosts were included, and it is possible that these were unusually gregarious birds that received lice from other birds more often through direct contact. If this is the case, we expect the measures in this study to be conservative estimates of genetic

differentiation for each louse species. We would expect the degree of structure to be even greater between louse subpopulations on pigeons with lower parasite loads.

Few empirical studies have rigorously investigated how particular life-history traits influence micro- and macroevolutionary patterns of diversification. One notable exception is a study by Riginos, Buckley, Blomberg, and Treml (2014) that links dispersal ecology with population genetic structure and species richness in reef fishes. Across these fish species, genetic differentiation and species richness are correlated with parental investment in larval dispersal. Members of fish families that guard eggs (low larval dispersal) have significantly more population structure and greater species richness than those that release eggs into the water column (high larval dispersal; Riginos et al., 2014). In other species, genome wide genetic diversity is known to correlate with different life-history strategies (Ellegren & Galtier, 2016; Romiguier et al., 2014). A thorough knowledge of species life-history strategies appears to be critical to accurately interpret patterns of population genetic differentiation (Rodriguez-Verdugo, Buckley, & Stapley, 2017; Weber, Wagner, Best, Harmon, & Matthews, 2017). Our study shows the importance of dispersal ecology in shaping differential patterns of genetic differentiation.

5 | CONCLUSION

Understanding how modes of dispersal affect genetic variation is important because population genetic structure influences rates of local adaptation, speciation and extinction. In addition, the influence of dispersal on genetic structure and metapopulation connectivity across landscapes is important for predicting how species respond to environmental change (Alberti, 2015; Cote et al., 2017; Hanski & Mononen, 2011; Legrand et al., 2017; Massol & Débarre 2015; Ronce, 2007). Theory predicts that the relative dispersal ability of interacting species plays a fundamental role in the resilience of ecological networks subject to environmental perturbations, such as climate change (Thompson & Gonzalez, 2017).

In this study, we found that nonphoretic body lice have more population genetic structure than phoretic wing lice. This pattern echoes what has been found at larger taxonomic, spatial and temporal scales. Among the different species of feather lice that are found on pigeons and doves of the world, body lice are more host-specific than wing lice, and they cospeciate with their hosts to a greater extent than wing lice (Clayton & Johnson, 2003; Clayton et al., 2015; Johnson & Clayton, 2003; Johnson et al., 2002). In short, our study is consistent with the hypothesis that phoretic dispersal plays a major role in shaping the coevolutionary dynamics of feather lice. Fly-mediated phoresis provides just one example of how even small differences in dispersal can influence population genetic patterns. Our study underscores that dispersal is integral in shaping the abundance and distribution of species and that examining dispersal-related life-history traits is critical in linking ecological processes with evolutionary patterns.

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DATA ACCESSIBILITY STATEMENT

Data are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.9t405v8). Data sets include genotypes for each species and input files for modelling analyses.

AUTHOR CONTRIBUTIONS

E.D., D.H.C., K.P.J. and S.E.B. conceived the study. E.D. performed the research and statistical analyses. A.N.H. and A.B.B. assisted with data collection. K.P.J. and S.E.B. contributed to data interpretation. E.D. wrote the first draft of the manuscript, and D.H.C., K.P.J., S.A.S. and S.E.B. contributed substantially to revisions.

ORCID

Emily DiBlasi http://orcid.org/0000-0002-1266-7297

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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