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Invited article

The influence of host dispersal on the gene flow and genetic diversity of generalist and specialist ectoparasites‡

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The dispersal and subsequent gene flow within parasite species is the result of a complex interaction between parasite life history, host life history and abiotic environmental factors. To gain more insights into the drivers responsible for parasite dispersal, COI mtDNA genetic data derived from six southern African generalist parasite species, including fleas, mites and ticks were compared with four specialist species from the same geographic region. Generalist tick species represented by *Amblyomma hebraeum*, *Hyalomma truncatum* and *H. rufipes* all occur temporarily on highly mobile ungulate hosts and showed high levels of haplotypic genetic diversity and high levels of dispersal with an average intraspecific global F_{st} (population differentiation index) value of 0.27 (±0.13). Generalist parasites, such as fleas, *Listropsylla agrippinae* and *Chiastopsylla rossi*, and one mite species, *Laelaps muricola*, that are all semi-permanent on the host and restricted to less mobile hosts species, showed a similar high level of genetic diversity, but an intermediate average F_{st} value of 0.67 (±0.11). Highly specialised semi-permanent parasites, such as the mite *L. giganteus* and the permanent lice *Polyplax praomydis*, *Hoplopleura patersoni* and *P. arvicanthis* recorded the lowest level of genetic diversity and a low level of gene flow among geographic sampling localities with an average F_{st} value of 0.95 (±0.05). This study provides strong support for the Specialist Generalist Variation Hypothesis (SGVH) and highlights the role that host dispersal and host specialisation by parasites play in the dispersal and evolution of ectoparasites.

Keywords: isolation by distance, mtDNA COI, population structure, southern Africa, Specialist Generalist Variation Hypothesis

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Introduction

Connectivity and subsequent gene flow among natural populations of species is one of the main factors maintaining conspecificity across a geographic range of a species. In the absence of sufficient gene flow among populations, genetic drift and selection can result in genetic divergence among populations that can ultimately contribute towards an allopatric speciation process (Schneider 2000; Huyse et al. 2005; Clegg and Phillimore 2010). For parasites, the factors affecting the dispersal and connectivity among populations are not well established (Barrett et al. 2008; van Schaik et al. 2014; DiBlasi et al. 2018). Through comparative phylogeographic studies between parasites and their hosts, it is evident that differences in parasite abundances on the hosts (Engelbrecht et al. 2016), ecological interactions between parasites (Cangi et al. 2013), and biogeographic conditions (Dick and Patterson 2007; du Toit et al. 2013; van der Mescht et al. 2015; Martinů et al. 2018; Stefan et al. 2018), can synergistically or separately all play a role in the dispersal and subsequent evolution of parasites. Given the close association between parasites and their hosts, and the fact that most terrestrial ectoparasite species are intrinsically not highly mobile, it is reasonable to suggest that host vagility will be a major contributing factor to facilitate parasite gene flow in terrestrial environments (Blasco-Costa, Waters and Poulin 2012; Araya-Anchetta et al. 2015; Matthee et al. 2018). In addition to host dispersal abilities, the life history of parasites and specifically also the host range (generalist or specialist) is probably equally important from an evolutionary point of view. Specialist parasites (those that can only survive on members of a single host species) often show more impediments to gene flow (high levels of genetic structure) and also often low levels of genetic diversity, a scenario best explained by the Specialist Generalist Variation Hypothesis (SGVH; Li et al. 2014; Matthee et al. 2018). The SGVH suggests that impediments to gene flow result from a lower prevalence of parasite habitat (host availability is less in host specific

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parasites), and lower levels of genetic diversity in specialist species are expected, because these taxa are more prone to local stochastic extinction events when members of their single host species experience local stochasticity (Li et al. 2014; Matthee et al. 2018).

To estimate the rate of dispersal and subsequent gene flow among populations of species is no trivial task (Huyse et al. 2005; Cayuela et al. 2018; Duranton et al. 2019). Furthermore, when studying inconspicuous and small-bodied taxa, such as the majority of parasites, dispersal rates have to be inferred and cannot rely on traditional methods, such as mark recapture and or telemetry. One commonly used indirect measure of migration among populations is to use the population differentiation index expressed as F_{st} (Wright 1949; Weir and Cockerham 1984). From the F_{st} equation it is possible to infer the number of migrants per breeding generation and F_{st} values range between zero (indicating complete panmixia) to one (indicating the complete absence of any movement inferred from the absence of any shared alleles). Although F_{st} values are useful measures to compare population genetic structure across species (Bohonak 1999; Medina et al. 2018), it is important to acknowledge that this population differentiation measure also relies on assumptions that can bias the results (Waples 1998; Whitlock and McCauley 1999; Huyse et al. 2005; Bhatia et al. 2013; Spies et al. 2018). Typically factors, such as differences in effective population size between species (Waples 1998; Huyse et al. 2005; Sovic et al. 2019), geographic range of the sampling localities (Steele et al. 2014), evolutionary rate of different markers (Willing et al. 2012; Zhou et al. 2013), and small sample sizes (Willing et al. 2012) can all make direct comparisons of F_{st} values among species problematic.

In the present study, global F_{st} values and haplotypic diversity of ten ectoparasite species, that differ in their life history and also sometimes utilise the same host species, were compared with each other. To limit some of the tribulations associated with F_{st} comparisons among species (Willing et al. 2012; Sovic et al. 2019), all these parasite taxa were represented by a reasonably large number of individuals (97–278; Table 1) and populations (6–25; Table 1), they were sampled in the same geographic region, and the COI and COII mtDNA molecular markers used show no dramatic intergene variability (Lopez et al. 1997). Three generalist (parasites completing their life cycle on multiple host species) tick species (*Amblyomma hebraeum*, *Hyalomma truncatum*, *Hyalomma rufipes*) that represent temporary parasites (parasites that are free-living during part of their life cycle) and whose adult stages commonly also occur on large mobile antelope and domestic ungulates (Cangi et al. 2013; Sands et al. 2017) are compared with two semi-permanent (parasites that utilise a host at one or more life stages, but some life stages are free living) generalist flea species (*Listropsylla agrippinae*, *Chiastopsylla rossi*) that exclusively occur on small rodents, shrews, and elephant shrews (Table 1; van der Mescht et al. 2015). Compared with the hosts of the tick taxa, the hosts of the flea species are less mobile; if host vagility is an important factor in parasite dispersion, then larger population differentiation values are expected for the fleas that occur on less mobile hosts. These five generalist parasites are compared with another generalist semi-permanent mite (*Laelaps muricola*) that is also restricted to rodents as hosts (Matthee et al. 2018) and to one host specific semi-permanent mite (*L. giganteus*), which is restricted to *Rhabdomys* spp. (Table 1; Engelbrecht et al. 2016). These parasitic taxa were then also compared with three permanent (a parasite that spends its entire life on its host), highly host specific, lice species (*Polyplax praomydis* and *Hoplopleura patersoni* that occur on *Michaleamys namaquensis* (Bothma et al. in review) and *P. arvicanthis* that occur exclusively on *Rhabdomys* spp. (Table 1; du Toit et al. 2013)). By drawing on comparative codivergence studies between parasites and their hosts (du Toit et al. 2013; Engelbrecht et al. 2016; Matthee et al. 2018; Bothma et al. in review) it is envisaged that the present comparative study can provide support for the generalisations that parasite host range (generalist versus specialist) and host dispersal ability are two of the main factors influencing parasite gene flow and diversity.

I hypothesise that host specific permanent parasites (such as lice) and those that are host specific, but not permanent (such as mites occurring mainly in the nest of the host), but which all occur on rodent hosts with limited dispersal capabilities, will show high levels of population differentiation and lower levels of genetic diversity. Generalist temporary parasites (such as ticks) occurring on both small mammals and large ungulates will show low levels of population differentiation and higher levels of genetic diversity (Li et al. 2014; Matthee et al. 2018). If the vagility of the host species is an important driver of parasite structure across the landscape, then it is reasonable to also hypothesise that generalist temporary species, such as fleas and some mites, only occurring on small mammals (rodents, shrews and elephant shrews) should show more genetic structure than ticks where some life stages also occur on highly mobile hosts (such as ticks and some mites; also see Araya-Anchetta et al. 2015).

Materials and methods

Data

Published mitochondrial DNA cytochrome oxidase I (COI) data (or in the case of the fleas COII), derived from 1 515 ectoparasites representing 10 different species were included in the present study (Table 1). All samples were collected from hosts occurring in southern Africa and, where relevant, ethical clearance and sampling permits were obtained and reported in the various publications (du Toit et al. 2013; van der Mescht et al. 2015; Engelbrecht et al. 2016; Bothma et al. in review). All sequence data were included from the published studies except in two instances. *Hyalomma truncatum* is a widely distributed species throughout Africa and show considerable population differentiation at the continental level (Sands et al. 2017) and in this instance only individuals in the southern African clade were included. In the case of *Polyplax arvicanthis,* two cryptic species with similar genetic patterns were detected and only lineage 2 (the most comprehensively sampled clade) was included (du Toit et al. 2013).

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Data analysis

Population differentiation values or global F_{st} values were calculated in Arlequin v. 3.5.2.2 (Excoffier and Lischer 2010). Although expressed as F_{st} in this paper, it is important to know that these values also take into account allelic evolutionary history (distances among different alleles) and strictly speaking therefore equate to Phi_{st} (ϕ) values (Excoffier et al. 1992). Nucleotide diversity (π) and haplotype diversity (*h*) values were obtained using DNASP v. 5 (Librado and Rozas 2009). To additionally depict dispersal across the landscape, five localities of each of the 10 species were selected based on their distances from one another. In an attempt to standardise the sampling, distances among populations range from a minimum of 50 km to a maximum of 1 079 km, and in instances where localities overlap, the same comparisons were included for multiple species. All comparisons were done among localities within previously detected monophyletic geographic clades to minimise differentiation, because of natural barriers to dispersal. The latter specifically pertains to *P. arvicanthis* and *L. giganteus* where only samples collected from *R. bechuanae* were used (du Toit et al. 2013; Engelbrecht et al. 2016). In the case of *H. truncatum* only samples from South Africa and Namibia were considered (Sands et al. 2017). Distances among sampling sites followed straight lines and were determined by plotting and measuring the sampling localities for each species in Google-Maps. Pairwise F_{st} values among sampling sites were obtained through an AMOVA analyses in Arlequin v. 3.5.2.2 (Excoffier and Lischer 2010). The natural log of the distance among these sites was then plotted against the pairwise F_{st} values between the sampling sites for each species, respectively. A regression analyses was performed in Microsoft Excel to visualise the effect of isolation by distance for the different parasite species.

Results

Global F_{st} values ranged from a low of 0.2 ($p < 0.05$) in the generalist temporary ticks *A. hebraeum* and *H. truncatum* to a high of 0.99 ($p < 0.05$) in the host specific permanent louse *H. patersoni* (Table 2). Generalist tick species with adult life stages that normally occur on highly mobile ungulates showed the lowest level of population differentiation with an average F_{st} value of 0.27 (±0.13), whereas intermediate levels of population structure was detected in fleas and some mites that are generalist temporary parasites occurring only on rodents and shrews (average F_{st} = 0.67, ±0.11; Table 2). Highly specialised permanent parasites showed the lowest level of gene

Table 1: Life history and the number of individuals and populations of each parasite species included in the present study. In each case the source of the sequence data is also indicated

Species (taxon designation)	N individuals (populations)	Parasitic mode (generalist/specialist)	Host range and permanency on the host	Source of data
Hyalomma truncatum (tick)	133 (10)	Generalist	2 host tick – temporary parasites. Juveniles occur on hares and ground feeding birds and adults utilise wild and domestic ungulates	Cangi et al. 2013
Amblyomma hebraeum (tick)	115 (6)	Generalist	3 host tick – temporary parasites. Small mammals, birds, reptiles, antelope and all domestic ruminants	Cangi et al. 2013
Hyalomma rufipes (tick)	162 (9)	Generalist	2 host tick – temporary parasites. Juveniles occur on hares and ground feeding birds and adults utilise wild and domestic ungulates	Sands et al. 2017
Chiastopsylla rossi (flea)	198 (19)	Generalist	Semi-permanent. Nest flea occurring on rodents, elephant shrews and shrews	Van der Mescht et al. 2015
Listropsylla agrippinae (flea)	126 (16)	Generalist	Semi-permanent. Fur flea occurring on rodents, elephant shrews and shrews	Van der Mescht et al. 2015
Laelaps muricola (mite)	109 (14)	Generalist	Semi-permanent. Nest parasite of various rodents	Matthee et al. 2017
Laelaps giganteus (mite)	278 (25)	Specialist	Semi-permanent. Nest parasite of *Rhabdomys* spp.	Engelbrecht et al. 2016
Polyplax arvicanthis (louse)	176 (17)	Specialist	Permanent parasite of *Rhabdomys* spp.	Du Toit et al. 2013
Polyplax praomydis (louse)	97 (8)	Specialist	Permanent parasite of *Micalaemys* spp.	Bothma et al. (in review)
Hoplopleura patersoni (louse)	121 (10)	Specialist	Permanent parasite of *Micalaemys* spp.	Bothma et al. (in review)

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Table 2: Genetic diversity and global F_{st} values for the ten ectoparasites species included in this study. In each case, it is indicated whether the species is a generalist or a specialist

Parasite species	Generalist/ specialist	mtDNA π (SD)	mtDNA h (SD)	Global F_{st}
Amblyomma hebraeum	Generalist	0.01 (±0.01)	0.66 (0.08)	0.20
Hyalomma truncatum	Generalist	0.07 (±0.04)	0.97 (0.09)	0.20
Hyalomma rufipes	Generalist	0.01 (±0.01)	0.96 (0.04)	0.43
Listropsylla agrippinae	Generalist	0.01 (±0.00)	0.93 (0.02)	0.77
Chiastopsylla rossi	Generalist	0.02 (±0.01)	0.96 (0.01)	0.70
Laelaps muricola	Generalist	0.02 (0.00)	0.97 (0.00)	0.56
Laelaps giganteus	Specialist	0.04 (0.00)	0.77 (0.03)	0.87
Polyplax arvicanthis	Specialist	0.09 (0.04)	0.85 (0.02)	0.96
Polyplax praomydis	Specialist	0.03 (0.01)	0.82 (0.02)	0.96
Hoplopleura patersoni	Specialist	0.07 (0.01)	0.91 (0.01)	0.99

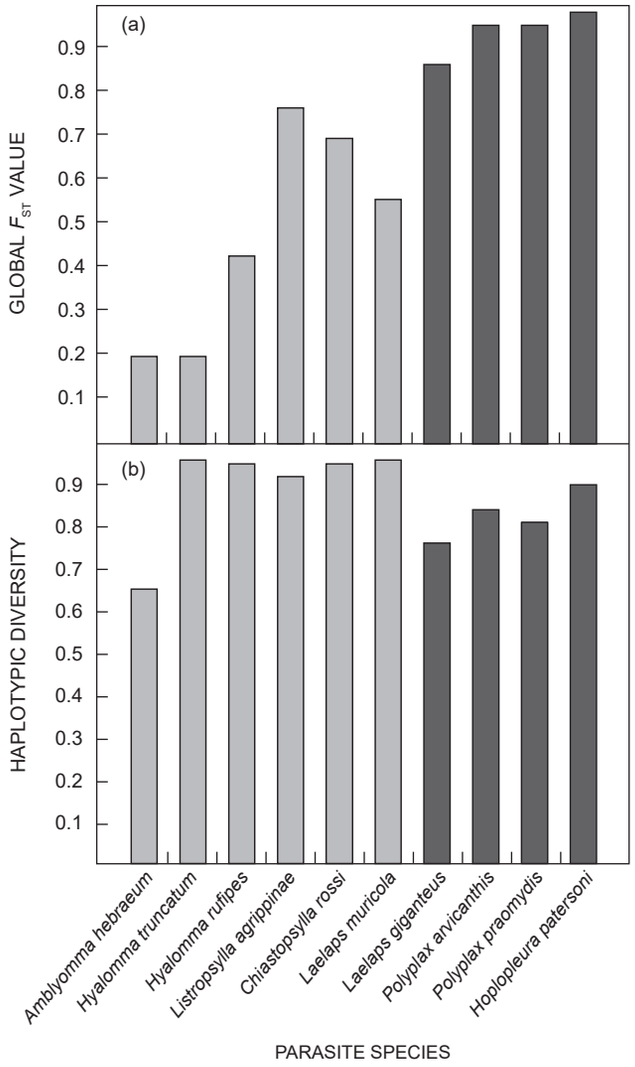


Figure 1: (a) Global F_{st} values for each species included in the present study. Species in light grey bars represent generalist parasites, whereas those in dark grey present specialist parasites, (b) Haplotypic diversity (*h*) values for each species sampled in the present study. Species in light grey bars represent generalist parasites, whereas those in dark grey present specialist parasites

flow among geographic sampling with an average F_{st} value of 0.95 (±0.05) among sampling localities (Table 2). Nucleotide diversities (π) were generally low and ranged from 0.01 (±0.01) in generalist parasites to 0.09 (±0.04) in a specialist (Table 2). Haplotypic diversity (*h*) also ranged from a low of 0.66 (±0.08) in a generalist tick *A. hebraeum* to a high of 0.97 (±0.01) in the generalist tick *H. truncatum* (Table 2). Apart from the generalist *A. hebraeum* showing a relatively low haplotypic diversity, there was a clear trend of higher haplotypic diversity values in generalist versus specialist species (Table 2; Figure 1). Average haplotypic diversity for generalist parasites was 0.91 (±0.12). Excluding *A. hebraeum*, which seemed to be an outlier, this average value for generalist parasites increased to h = 0.95 (±0.02). Specialists showed a lower level of heterozygosity with an average h = 0.84 (±0.06). Nucleotide diversity values did not show any marked trend that could be associated with the generalist or specialist parasites sampled in this study (Table 2).

The generalist tick species included herein showed weak relationships between geographic distance and F_{st} values (cf. R^2 = 0.05 for *H. truncatum* and R^2 = 0.29 for *H. rufipes*), whereas the permanent host specific louse *H. patersoni* occurring on *M. namaquensis* showed the steepest isolation by distance slope and a much better linear relationship between F_{st} and geographic distance (R^2 = 0.90; Figure 2). Generalist species, such as the fleas that only utilise small mammals during their life cycle and do not occur permanently on the host, showed more congruence with isolation by distance (R^2 = 0.60 and 0.87, respectively) than the generalist ticks that also utilise larger ungulates as part of their life cycle. In the case of the nest generalist, *L. muricola*, the relationship between geographic distance and genetic divergence was weak (R^2 = 0.16; Figure 2).

Discussion

Gene flow in ectoparasites is regarded as the result of a complex interaction between host dispersal abilities and host specialisation (Appelgren et al. 2018; Wessels et al. 2019), landscape effects (Nieberding et al. 2008; du Toit et al. 2013; Talbot et al. 2017) and other parasite life history traits, such as the ability of the parasite to switch hosts (du Toit et al. 2013; Engelbrecht et al. 2016), presence of

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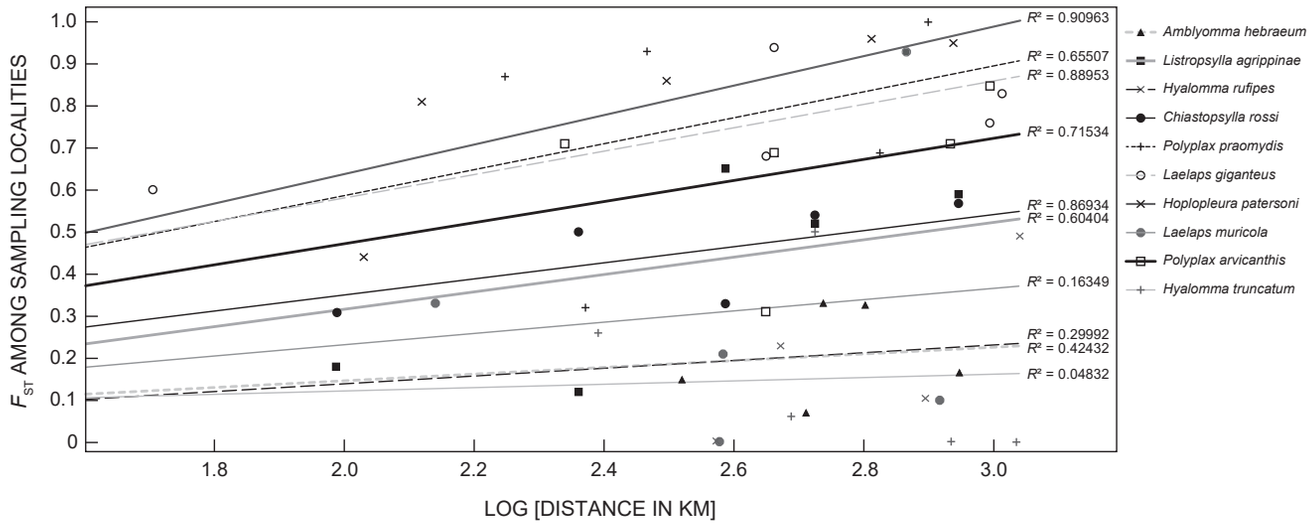


Figure 2: Scatterplots, indicating the log of the geographic distance against global F_{st} values. The optimal linear relationship is indicated for each species together with the R^2 value for each linear fit. Species names are indicated for each regression

interspecific competition limiting host availability (Cangi et al. 2013) and time spent on the host (van der Mescht et al. 2015). A comprehensive review, including 22 tick species with different life histories and host specialisations revealed that 50% of the taxa studied showed a close correlation between genetic structure and the movement capacity of hosts (Araya-Anchetta et al. 2015). For example, gene flow was lower in taxa that utilise smaller bodied less mobile hosts, when compared with taxa utilising more mobile larger hosts. In the remainder of the taxa, however, behavioural limitations played a major role in the genetic structure of species (Araya-Anchetta et al. 2015).

From the above, and other studies (Blasco-Costa et al. 2012; Matthee et al. 2018), it is reasonable to suggest that although gene flow in ectoparasites can be strongly influenced by host vagility, other factors, such as abiotic vicariance processes and parasite life history, also play a role (also see Engelbrecht et al. 2016). In the present study, both host vagility and host range (level of host specificity) are strongly correlated with the amount of gene flow among geographic populations. There was a strong correlation between host range and host mobility, and the F_{st} values among the 10 parasites compared herein. Low F_{st} values (ranging from 0.20 to 0.43) were present in the three tick species with a wide host range and which all utilise large ungulates for their adult stages. Intermediate F_{st} values (ranging from 0.56 to 0.77) were detected in other generalist species, such as the fleas and *L. muricola* that mainly utilise small rodents and shrews, whereas high F_{st} values (> 0.87) were present in the specialist mite (*L. giganteus*) and the three specialist lice all occurring on single rodent species (Table 2; Figure 1). Effective population sizes, however, can influence the F_{st} values obtained (Huyse et al. 2005). Generally species with small effective population sizes tend to have elevated F_{st} values, whereas species with larger effective population sizes will have comparatively lower F_{st} values (Nadler 1995). Unfortunately, effective population size estimates for the species sampled herein do not readily exist, but it is interesting to note that in other studies, ticks of the genus *Amblyomma* showed low effective population sizes locally (Huber et al. 2019), whereas fleas showed higher effective population sizes (Harimalala et al. 2017). If this holds true, the differences in F_{st} estimates among the 10 parasite species sampled herein, unambiguously point to a strong influence of host vagility and host range in the dispersal and subsequent gene flow in parasites (also see Araya-Anchetta et al. 2015).

The relationship between host dispersal and parasite dispersal is also reflected by the isolation by distance comparisons among the 10 parasite species. The four species that showed the weakest isolation by distance, as shown by the R^2 values (ranging from 0.04 to 0.42 in *H. rufipes, H. truncatum, A. hebraeum* and *L. muricola*), are generalists occurring on either highly mobile hosts, such as ungulates, or in the case of the mite, *L. muricola*, on several small rodents, but particularly also on *Mastomys natalensis* and *M. coucha* (Sands et al. 2014; Matthee et al. 2018). The majority of the hosts of these four generalists show panmictic or shallow population structures with admixture among geographic areas within their southern African range (Lorenzen et al. 2012; Sands et al. 2014). In the case of the flea taxa included herein, that are also generalists, there is a stronger pattern of isolation by distance (R^2 = 0.6 − 0.86). In the latter case, however, the common hosts of these parasites are all rodents documented to show phylogeographic structure throughout their range (host species for the fleas include *Rhabdomys* spp. – du Toit et al. 2012; *Micaelamys* spp. – Russo et al. 2010; *Otomys* spp. – Engelbrecht et al. 2011; *Myotomys* spp. – Edwards et al. 2011; *Myosorex* spp. – Willows-Munro and Matthee 2011; *Elephantulus* spp. – Smit et al. 2007). In line with the trend, the four specialist species also occur on geographically structured hosts *Rhabdomys* spp. and *Micaelamys* spp. and again they show a stronger pattern of isolation by distance (R^2 range from 0.65 to 0.91). Overall,

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these findings support the effect of host mobility on the gene flow of ectoparasites (also see Araya-Anchetta et al. 2015).

In small isolated populations inbreeding and bottlenecks will reduce intraspecific genetic variability (Nei et al. 1975; Charlesworth 2003; Huyse et al. 2005). A high level of migration and subsequent gene flow throughout the landscape will conversely maintain intraspecific genetic diversity (Slatkin 1985; Song et al. 2013). In parasites, the effective population sizes are generally smaller than those of the hosts (Huyse et al. 2005; Harimalala et al. 2017) and intraspecific genetic diversity is therefore also predicted to be more severely reduced by population fluctuations. Along these lines, host specific parasites will show the lowest genetic diversity, because they depend on a single host for survival, whereas generalists will show higher genetic diversity, because their population numbers are most likely more stable across the landscape (Li et al. 2014). With the exception of *A. hebraeum*, all generalists included herein have higher inferred genetic diversity ($h \geq 0.93$) than found in the specialist ($h \leq 0.91$). The reason(s) for the comparatively low haplotypic diversity in the generalist tick, *A. hebraeum*, is not clear. In fact, this tick species is more of a generalist when compared with *H. rufipes* (Cangi et al. 2003). The most plausible speculative explanation for the low genetic diversity in *A. hebraeum* may be linked to a comparatively small occupancy range of the species and also interspecific competition with the more widely distributed *A. variegatum* (Bournez et al. 2015). If *A. hebraeum* is exposed to more severe population fluctuations than the other two generalist tick species sampled in the present study, their genetic diversity will be comparatively lower. Irrespective of this discrepancy, when population structure and genetic diversity for the 10 parasites studied herein are considered, there is nearly 100% (with the exception of the genetic diversity in *A. hebraeum*) support for the SGVH (Li et al. 2014; Matthee et al. 2018).

The present study contributes to our understanding of some of the uncertainties surrounding the mechanisms involved in the dispersal and subsequent gene flow of ectoparasites. Although it is well documented that a variety of factors influence the dispersal of parasites (Nieberding et al. 2008; Cangi et al. 2013; du Toit et al. 2013; van der Mescht et al. 2015; Engelbrecht et al. 2016; Talbot et al. 2017; Appelgren et al. 2018; Wessels et al. 2019), the present comparative study highlight the important roles that host dispersal abilities and host specialisetion can play in the evolution of ectoparasites. Generalist temporary parasites occurring on highly mobile hosts showed a low level of population structure and a high level of genetic diversity, whereas specialist permanent parasites occurring on hosts that are also genetically structured throughout the landscape showed a high level of population differentiation and a lower level of genetic diversity.

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References

Araya-Anchetta A, Busch JD, Scoles GA, Wagner DM. 2015. Thirty years of tick population genetics: a comprehensive review. *Infection, Genetics and Evolution* 29: 164–179. https://doi.org/10.1016/j.meegid.2014.11.008.

Appelgren ASC, Saladin V, Richner H, Doligez B, McCoy KD. 2018. Gene flow and adaptive potential in a generalist ectoparasite. *BMC Evolutionary Biology* 18: 99. https://doi.org/10.1186/s12862-018-1205-2.

Barrett LG, Thrall PH, Burdon JJ, Linde CC. 2008. Life history determines genetic structure and evolutionary potential of host–parasite interactions. *Trends in Ecology & Evolution* 23: 678–685. https://doi.org/10.1016/j.tree.2008.06.017.

Blasco-Costa I, Waters JM, Poulin R. 2012. Swimming against the current: genetic structure, host mobility and the drift paradox in trematode parasites. *Molecular Ecology* 21: 207–217. https://doi.org/10.1111/j.1365-294X.2011.05374.x.

Bohonak AT. 1999. Dispersal, Gene Flow, and Population Structure. *The Quarterly Review of Biology* 74: 21–45. https://doi.org/10.1086/392950.

Bothma JC, Matthee S, Matthee CA. (in review). Comparative phylogeography between parasitic sucking lice and their host the Namaqua rock mouse, *Micaelamys namaquensis* (Rodentia: Muridae). *Zoological Journal of the Linnean Society.*

Bournez L, Cangi N, Lancelot R, Pradel DR, Stachurski F, Bouyer J, Martinez D, Lefrancois T, Neves L, Pradal J. 2015. Parapatric distribution and sexual competition between two tick species, *Amblyomma variegatum* and *A. hebraeum* (Acari, Ixodidae), in Mozambique. *Parasites & Vectors* 8: 504. https://doi.org/10.1186/s13071-015-1116-7.

Cangi N, Horak IG, Apanaskevich DA, Matthee S, das Neves LCB, Estrada- Peña A, Matthee CA. 2013. The influence of interspecific competition and host preference on the phylogeography of two African ixodid tick species. *PloS one* 8(10): e76930. https://doi.org/10.1371/journal.pone.0076930.

Cayuela H, Rougemont Q, Prunier JG, Moore JS, Clobert J, Besnard A, Bernatchez L. 2018. Demographic and genetic approaches to study dispersal in wild animal populations: A methodological review. *Molecular Ecology* 27: 3976–4010. https://doi.org/10.1111/mec.14848.

Charlesworth D. 2003. Effects of inbreeding on the genetic diversity of populations. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 358: 1051–1070. https://doi.org/10.1098/rstb.2003.1296.

Clegg SM, Phillimore AB. 2010. The influence of gene flow and drift on genetic and phenotypic divergence in two species of *Zosterops* in Vanuatu. *Philosophical Transactions of the Royal Society B* 365: 1077–1092. https://doi.org/10.1098/rstb.2009.0281.

DiBlasi E, Johnson KP, Stringham SA, Hansen AH, Beach AB, Clayton DH, Bush SE. 2018. Phoretic dispersal influences parasite population genetic structure. *Molecular Ecology* 27: 2770–2779. https://doi.org/10.1111/mec.14719.

Dick CW, Patterson BD. 2007. Against all odds: Explaining high host specificity in dispersal-prone parasites. *International Journal for Parasitology* 37: 871–876. https://doi.org/10.1016/j.ijpara.2007.02.004.

Duranton M, Bonhomme F, Gagnaire P. 2019. The spatial scale of dispersal revealed by admixture tracts. *Evolutionary Applications* 12: 1743–1756. https://doi.org/10.1111/eva.12829.

Edwards S, Claude J, van Vuuren BJ, Matthee CA. 2011

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Evolutionary history of the Karoo bush rat, *Myotomys unisulcatus* (Rodentia: Muridae): Disconcordance between morphology and genetics *Biological Journal of the Linnean Society. Linnean Society of London* 102: 510–526. https://doi.org/10.1111/j.1095-8312.2010.01583.x.

du Toit N, Jansen van Vuuren B, Matthee S, Matthee CA. 2012. Biome specificity of distinct genetic lineages within the four-striped mouse *Rhabdomys pumilio* (Rodentia: Muridae) from southern Africa with implications for taxonomy. *Molecular Phylogenetics and Evolution* 65: 75–86. https://doi.org/10.1016/j.ympev.2012.05.036.

du Toit N, Jansen van Vuuren B, Matthee S, Matthee CA. 2013. Biogeography and host-related factors trump parasite life-history: limited congruence among the genetic structures of specific ectoparasitic lice and their rodent hosts. *Molecular Ecology* 22: 5185–5204. https://doi.org/10.1111/mec.12459.

Engelbrecht A, Taylor PJ, Daniels SR, Rambau RV. 2011. Cryptic speciation in the southern African vlei rat *Otomys irroratus* complex: evidence derived from mitochondrial cyt b and niche modelling. *Biological Journal of the Linnean Society. Linnean Society of London* 104: 192–206. https://doi.org/10.1111/j.1095-8312.2011.01696.x.

Engelbrecht, A, Matthee S, du Toit, N, Matthee CA. 2016. Limited dispersal in an ectoparasitic mite*, Laelaps giganteus*, contributes to significant phylogeographic congruence with the rodent host, *Rhabdomys. Molecular Ecology* 25: 1006–1021. https://doi.org/10.1111/mec.13523.

Excoffier L, Lischer HEL. 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources* 10: 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x.

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.

Harimalala M, Telfer S, Delatte H, Watts PC, Miarinjara A, Ramihangihajason TR, Rahelinirina S, Rajerison M, Boyer S. 2017. Genetic structure and gene flow of the flea *Xenopsylla cheopis* in Madagascar and Mayotte. *Parasites & Vectors* 10: 347. https://doi.org/10.1186/s13071-017-2290-6.

Huber K, Jacquet S, Rivallan R, Adakal H, Vachiery N, Risterucci AM, Chevillon C. 2019. Low effective population sizes in *Amblyomma variegatum*, the tropical bont tick. *Ticks and Tick-Borne Diseases* 10: 93–99. https://doi.org/10.1016/j.ttbdis.2018.08.019.

Huyse T, Poulin R, Théron A. 2005. Speciation in parasites: a population genetics approach. *Trends in Parasitology* 21: 469–475. https://doi.org/10.1016/j.pt.2005.08.009.

Li S, Jovelin R, Yoshiga T, Tanaka R, Cutter AD. 2014. Specialist versus generalist life histories and nucleotide diversity in Caenorhabditis nematodes. *Proceedings. Biological Sciences* 281: 2858.

Librado P, Rozas J. 2009. DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics (Oxford, England)* 25: 1451–1452. https://doi.org/10.1093/bioinformatics/btp187.

Lorenzen ED, Heller R, Siegismund HR. 2012. Comparative phylogeography of African savanna ungulates. *Molecular Ecology* 21: 3656–3670. https://doi.org/10.1111/j.1365-294X.2012.05650.x.

Martinů J, Hypša V, Štefka J. 2018. Host specificity driving genetic structure and diversity in ectoparasite populations: Coevolutionary patterns in *Apodemus* mice and their lice. *Ecology and Evolution* 8: 10008–10022. https://doi.org/10.1002/ece3.4424.

Matthee CA, Engelbrecht A, Matthee S. 2018. Comparative phylogeography of parasitic *Laelaps* mites contribute new insights into the specialist-generalist variation hypothesis (SGVH). *BMC Evolutionary Biology* 18: 131. https://doi.org/10.1186/s12862-018-1245-7.

Medina I. Cooke GM, Ord TJ. 2018. Walk, swim or fly? Locomotor mode predicts genetic differentiation in vertebrates. *Ecology Letters*: 638. https://doi.org/10.1111/ele.12930.

Nadler SA. 1995. Microevolution and the genetic structure of parasite populations. *The Journal of Parasitology* 81: 395–403. https://doi.org/10.2307/3283821.

Nei M, Maruyama T, Chakraborty R. 1975. The bottleneck effect and genetic variability in populations. *Evolution; International Journal of Organic Evolution* 29: 1–10. https://doi.org/10.1111/j.1558-5646.1975.tb00807.x.

Nieberding CM, Durette-Desset MC, Vanderpoorten A, Casanova JC, Ribas A, Deffontaine RV, Feliu C, Morand S, Libois R, Michaux JR. 2008. Geography and host biogeography matter for understanding the phylogeography of a parasite. *Molecular Phylogenetics and Evolution* 47: 538–554. https://doi.org/10.1016/j.ympev.2008.01.028.

Russo IRM, Chimimba CT, Bloomer P. 2010. Bioregion heterogeneity correlates with extensive mitochondrial DNA diversity in the Namaqua rock mouse, *Micaelamys namaquensis* (Rodentia: Muridae) from southern Africa-evidence for a species complex. *BMC Evolutionary Biology* 10: 307. https://doi.org/10.1186/1471-2148-10-307.

Sands AF, Apanaskevich DA, Matthee S, Horak IG, Matthee CA. 2017. The effect of host vicariance and parasite life history on the dispersal of the multi-host ectoparasite, *Hyalomma truncatum. Journal of Biogeography* 44: 1124–1136. https://doi.org/10.1111/jbi.12948.

Sands AF, Matthee S, Mfune JKE, Matthee CA. 2015. The influence of life history and climate driven diversification on the mtDNA phylogeographic structures of two southern African *Mastomys* species (Rodentia: Muridae: Murinae). *Biological Journal of the Linnean Society. Linnean Society of London* 114: 58–68. https://doi.org/10.1111/bij.12397.

Slatkin, M. 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics* 16: 393–430. https://doi.org/10.1146/annurev.es.16.110185.002141.

Smit HA, Robinson TJ, van Vuuren BJ. 2007. Coalescence methods reveal the impact of vicariance on the spatial genetic structure of *Elephantulus edwardii* (Afrotheria, Macroscelidea). *Molecular Ecology* 16: 2680–2692. https://doi.org/10.1111/j.1365-294X.2007.03334.x.

Song G, Yu LJ, Gao B, Zhang RY, Qu YH, Lambert DM, Li SH, Zhou TL, Lei FM. 2013. Gene flow maintains genetic diversity and colonization potential in recently range-expanded populations of an Oriental bird, the Light-vented bulbul (*Pycnonotus sinensis*, Aves: Pycnonotidae). *Diversity & Distributions* 19: 1248–1262. https://doi.org/10.1111/ddi.12067.

Steele CD, Court DS, Balding DJ. 2014. Worldwide Fst estimates relative to five continental-scale populations. *Annals of Human Genetics* 78: 468–477. https://doi.org/10.1111/ahg.12081.

Spies I, Hauser L, Jorde PE, Knutsen H, Punt AE, Rogers LA, Stenseth NC. 2018. Inferring genetic connectivity in real populations, exemplified by coastal and oceanic Atlantic cod. *Proceedings of the National Academy of Sciences of the United States of America* 115: 4945–4950. https://doi.org/10.1073/pnas.1800096115.

Schneider CJ. 2000. Natural selection and speciation. *Proceedings of the National Academy of Sciences of the United States of America* 97: 12398–12399. https://doi.org/10.1073/pnas.240463297.

Sovic MG, Fries A, Martin SA, Lisle Gibbs H. 2018. Genetic signatures of small effective population sizes and demographic declines in an endangered rattlesnake, *Sistrurus catenatus*. *Evolutionary Applications* 12: 664–678. https://doi.org/10.1111/eva.12731.

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Stefan LM, Gómez-Díaz E, Mironov SV, González-Solís J, McCoy KD. 2018. More than meets the eye: Cryptic diversity and contrasting patterns of host-specificity in feather mites inhabiting seabirds. *Frontiers in Ecology and Evolution* 6: 97. https://doi.org/10.3389/fevo.2018.00097.

Talbot B, Vonhof MJ, Broders HG, Fenton B, Keyghobadi N. 2017. Comparative analysis of landscape effects on spatial genetic structure of the big brown bat and one of its cimicid ectoparasites. *Ecology and Evolution* 7: 8210–8219. https://doi.org/10.1002/ece3.3329.

van der Mescht L, Matthee S, Matthee CA. 2015. Comparative phylogeography between two generalist flea species reveal a complex interaction between parasite life history and host vicariance: Parasite-host association matters. *BMC Evolutionary Biology* 15: 105. https://doi.org/10.1186/s12862-015-0389-y.

van Schaik J, Kerth G, Bruyndonckx N, Christe P. 2014. The effect of host social system on parasite population genetic structure: comparative population genetics of two ectoparasitic mites and their bat hosts. *BMC Evolutionary Biology* 14: 18. https://doi.org/10.1186/1471-2148-14-18.

Waples RS. 1998. Separating the wheat from the chaff: Patterns of genetic differentiation in high gene flow species. *The Journal of Heredity* 89: 438–450. https://doi.org/10.1093/jhered/89.5.438.

Weir BS, Cockerham CC. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 38: 1358–1370.

Wessels C, Matthee S, Espinaze MPA, Matthee CA. 2019. Comparative mtDNA phylogeographic patterns reveal marked differences in population genetic structure between generalist and specialist ectoparasites of the African penguin. Parasitology Research 118: 667–672. https://doi.org/10.1007/s00436-018-6150-x.

Whitlock MC, McCauley DE. 1999. Indirect measures of gene flow and migration: $F_{st} \neq 1/(4Nm+1)$. *Heredity* 82: 117–25. https://doi.org/10.1038/sj.hdy.6884960.

Willing EM, Dreyer C, van Oosterhout C. 2012. Estimates of genetic differentiation measured by F(ST) do not necessarily require large sample sizes when using many SNP markers. *PLoS ONE* 7: e42649. https://doi.org/10.1371/journal.pone.0042649.

Willows-Munro S, Matthee CA. 2011. Linking lineage diversification to climate and habitat heterogeneity: Phylogeography of the southern African shrew *Myosorex varius*. *Journal of Biogeography* 38: 1976–1991. https://doi.org/10.1111/j.1365-2699.2011.02543.x.

Wright S. 1949. The genetical structure of populations. *Annals of Human Genetics* 15: 323–354.

Zhou X, Xie Y, Zhang Z, Wang C, Sun Y, Gu X, Wang S, Peng X, Yang G. 2013. Analysis of the genetic diversity of the nematode parasite *Baylisascaris schroederi* from wild giant pandas in different mountain ranges in China. *Parasites & Vectors* 6: 233. https://doi.org/10.1186/1756-3305-6-233.

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