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Parasitism and speciation in a changing world

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Introduction to parasitism

What is a parasite?

Parasitism is one of the most common life-history strategy in nature with almost every species being susceptible to infection by another (Windsor 1988). Parasitism as a trait conveys many benefits, including a stable environment and a direct food supply for the parasite. However, these benefits are detrimental to the host as nutrients are diverted towards the parasite and a costly immune system is required to fight and control them. Indeed, the benefits of parasitism are so great that many parasites have their own parasites, such as the hyperparasitoid wasps (Van Nouhuys & Hanski, 2000), where female wasps search for and lay their eggs in the larvae of other parasitic wasps, within previously occupied hosts. Parasites and their hosts are often described to be in an evolutionary “arms-race”. In this model, as a parasite infects a host, the host evolves a defensive immune response or develops other barriers to combat the parasite. This exerts strong selective pressure on both hosts and parasites and can lead to very rapid co-evolution of infection ability and defences (Woolhouse et al., 2002).

Parasitism comes in many overlapping forms and functional categories, in part due to the diverse range of taxa which have evolved the trait. Microparasites are usually defined as small (<200µm in length), they are fast growing and have short generation times and can quickly multiply to large numbers in their host. Epidemiologically, they are not considered as individual units, and replication rate and infection intensity is used to assess their effects on the host. Macroparasites are larger, multicellular organisms with longer generation times. Their growth rate is often considered to be as important a measure as their infection intensity. Parasitoids are slightly different to the previous two categories as they are sometimes not classed as true parasites. This is because they have a free-living stage (usually the adult), free from a host. Another reason why many parasitoids are not considered true parasites is that their parasitic phase results in the obligate death of their host. These three categories can be further classed as endo- or ectoparasites. Endoparasites live within the host, such as in the bloodstream or intracellularly. Most microparasites fall into this category, as do many parasitoids. Ectoparasites live outside or on the host, for instance attached to the skin or within the digestive tract. As a result, most ectoparasites are macroparasites. The final category of parasites are the social parasites. These exploit the social systems of other organisms and can range from commensal species to kleptoparasites and nest-parasites. They are typically macroparasites and this category is typically the loosest and furthest derived from the strictest definitions of parasitism. In-depth descriptions of different modes of parasitism and their costs and

benefits to both hosts and parasites can be found in the excellent book on evolutionary parasitology by Schmid-Hempel, 2011.

Parasites are a strong selective agent that can both promote and constrain host diversification. In a study by Bucking and Rainey (2002), Sympatric populations of the bacteria *Pseudomonas fluorescens* had reduced diversity in the presence of viral phages as host density was decreased, allowing for reduced resource competition and niche partitioning. In contrast, allopatric populations showed greater diversity as host-parasite arms races drove replicates on different evolutionary trajectories. This can also have a role in mediating the strength of secondary sexual characteristics, as parasitic infections can limit the expression of sexually selected traits (Hamilton & Zuk, 1982; Møller & Saino, 1994). This can, in turn, strengthen reproductive isolation if there is a divergence of preference in mate choice. Despite the extensive theoretical background, (Able, 1996; Clayton & Moore, 1997) there have been very few empirical examples. Mate choice in Lake Victoria cichlids (Maan et al., 2008) is one notable example where two sister species of haplochromine cichlid species male nuptial colour divergence with *Pundamilia pundamilia* displaying metallic blue patterning and *P. nyererei* displaying carotenoid-based yellow and red patterning. *P. nyererei* is infected with a higher diversity of parasites, leading to more exaggerated and costly patterning via female mate choice. Therefore parasite-mediated mate choice may strengthen reproductive isolation.

The immune response

Hosts have evolved many strategies to deal with infections by parasites such as parasite avoidance, post-infection behaviours and immune response (innate and adaptive). The innate immune system refers to non-specific mechanisms that act as barriers to infection. This includes immune system cells like neutrophils or structures such as skin. More specific examples include melanisation processes in arthropods (Marmaras et al., 1996; Jiravanichpaisal et al., 2006). The adaptive immune system is more complex and targets specific pathogens or parasites. The underlying genetic basis of the adaptive immune system are the major-histocompatibility complex (MHC) genes. These code for a series of cell-surface proteins that are able to recognise and target different pathogens. MHC diversity is crucial for defence against multiple parasites and diversity is strongly selected for, even in bottlenecked populations (Richardson & Westerdahl, 2003). There are three main selection mechanisms that have been proposed: heterozygote advantage; rare-allele advantage and fluctuating selection. The heterozygote advantage hypothesis states that individuals with higher heterozygosity for MHC genes will be able to defend against a greater range of parasites

then homozygous individuals. This will increase host fitness and MHC diversity will be maintained. This has been demonstrated by studies such as Penn et al. (2002) in mice. The rare-allele hypothesis is based in the theory of negative frequency dependence. This hypothesis suggests that rare and novel MHC alleles will confer a greater selective advantage over pathogens than common ones. As the rare allele increases in the population, parasites will evolve to counteract its effects. This co-evolutionary arms-race creates a dynamic system of MHC diversity as allele frequencies rise and fall over time (Slade & McCallum, 1992). Fluctuating selection theory suggests that MHC diversity varies both spatially and temporally. This suggests that parasites and hosts do not necessarily overlap in their ranges so that different MHC genes are beneficial in different locations or times (Hendrick, 2002). This theory can be separated from negative-frequency dependence models by its reliance on selection being directional rather than cyclical. These three hypotheses are not necessarily mutually exclusive. For example, modelling has shown that heterozygote advantage alone, cannot explain the extent of MHC polymorphisms and that fitness contributions of each allele need to be taken into account (De Boer et al., 2004). Additionally, the rare-allele hypothesis and fluctuating selection are complementary to each other as negative-frequency dependence is important if parasite diversities change over time. A review by Spurgin and Richardson (2010) covers the extent and limits of these theories and gives empirical examples.

MHC genes can even act as magic traits (traits which facilitate speciation with gene-flow, when traits leading to divergent selection also contribute to non-random mating) whereby MHC diversity can be detected via olfactory cues leading to non-random mate-choice. This has been demonstrated in populations of three-spined sticklebacks (*Gasterosteus aculeatus*) (Eizaguirre et al., 2009; Eizaguirre et al., 2011). This offers a tantalising insight into the potential indirect role of parasites in host speciation, as different communities of parasites lead to variation in MHC diversity on a geographic scale.

Parasitism in a changing world

Parasites and interspecific interactions

Parasites are adept at modifying and manipulating host behaviour and physiology. This can be both passive and active. Active effects are very common in nature and cause behavioural changes in the host that are adaptive for the parasite, often at a cost to the host. *Tylodephys* trematodes infect the eyes of a fish, the common bully (*Gobiomorphus cotidianus*). The parasite

increases optical obstruction in the fish during daylight hours, during which, they are more susceptible to predation by avian predators (Stumbo & Poulin, 2016). This increases the chance of the fish being predated during the day which is beneficial for the parasite as an avian host is an obligate stage in their life-cycle. By reducing the obstruction during the night, they lower the chance of the fish being predated by other predators. Another example are the *Ophiocordyceps* fungi that infect various species of ants. The fungus invades the nervous system of the host ant causing it to climb into trees. There the fungus kills the host and produces fruiting bodies which drop spores onto other potential host ants (Shang et al., 2015).

Many parasites are able to infect multiple host species. However, the virulence of the parasite can vary between species which can have interesting implications for interspecific interactions. Laboratory experiments with two species of *Tribolium* beetle have shown that *T. castaneum* consistently drives *T. confusum* to extinction. However, in the presence of the protozoan parasite *Adelina tribolii*, both beetle species are able to co-exist, as the parasite is more infectious in the better competitor (Park, 1948). However in the same system, a different parasite species, the tapeworm *Hymenolepis diminuta* is more virulent in the poorer competitor of the two beetles, driving it to extinction faster (Yan et al., 1998). Similar examples have been found in field studies, where avian malaria exacerbates competitive asymmetry in two *Ficedula* flycatchers (Kulma, et al., 2013).

Hybrids and parasites

Hybridisation has often been neglected in speciation research due to the low fitness of hybrids. However, the role of hybridisation in species maintenance and its role in speciation is increasingly being appreciated (Buckling & Rainey, 2002).

A study by Guttel and Ben-Ami (2014) showed that parasites help to maintain hybrids. Hybrids of two *Melanopsis* snail species had lower infection rates by trematodes than either parental species. Hybrids were also not susceptible to symptoms such as parasite-induced gigantism that were more common in the parental species. Hybrids also survived better in extreme environments. Trematodes infect and destroy host gonads, which theoretically causes the host to reallocate resources to other areas such as growth, which is the authors' explanation for the lack of gigantism in hybrids. Coupled with the higher heterogeneity of hybrid immune genes, this explains their reduced effects and infection rates. However, these results could be unusual given the high fitness costs of parasitic infection for the parental species.

Conversely, hybrid mouse lemurs (*Microcebus sp.*) carry higher nematode burdens than any of the three parent species (Sommer et al., 2014). All three species occupy different habitats, with

Microcebus murinus occupying dry, spiny forest; *M. griseorufus* in spiny and gallery forest and *M. rufus* in humid rain forest; however there is significant levels of sympatry and hybridisation at ecotones between *M. murinus* and *M. griseorufus*. Patterns of infection intensity could not be explained purely by differential infection rates between habitats, where nematode abundance varies with humidity, with the rain forests harbouring the highest parasite densities (Bohr et al., 2011; Sommer et al., 2014). The higher costs associated with this have maintained species barriers in three sympatric species (Sommer et al., 2014).

If we take a theoretical example of two species evolving in allopatry and then coming into secondary contact, MHC diversity may play a vital role in the maintenance of species boundaries. If hybridisation occurs, then MHC diversity will be increased. This will lead to a reduction in the symptoms on infection and increased hybrid fitness. Therefore hybridisation will become adaptive and the two lineages will merge to form a new hybrid species. This scenario may be played out in the case of the *Melanopsis* snails (Guttel & Ben-Ami, 2014). However, more is not always better with MHC diversity. If heterogeneity is too high in hybrids then hybridisation will be maladaptive and the two species will be maintained (Eizaguirre et al., 2009). This is the likely outcome of the *Microcebus* lemur system (Sommer et al., 2014). This process may be exacerbated if, at the earlier stages of secondary contact, hybrid fitness could result in the introgression of novel MHC genes, thereby increasing the MHC diversity of each parental species and a corresponding increase in fitness. This has been shown in *Lissotriton* newts (Nadachowska-Brzyska et al., 2012) where hybridisation has led to the successful introgression of MHC genes between *Lissotriton vulgaris* and *Lissotriton montandoni*.

Parasites and climate change

Global climate change is causing environments to change at unprecedented rates (McCarty, 2001). As a result the distributions of many species are changing or are predicted to change to cope with these factors. As hosts move, their parasites are brought with them and can potentially cross over to closely related species (Brooks & Hoberg, 2007; Lafferty, 2009). Due to the rapid evolution of host-parasite interactions, many new hosts may be unequipped to deal with a different parasite community. For example, warmer temperatures have been identified as the leading cause in global amphibian declines and extinctions as fungal diseases spread (Pounds et al., 2006; Bosch et al., 2007). However, climate change can also effect a species ability to mount an immune response to parasites already in their range. One such study by Hudson et al., (2006) illustrates this elegantly. European rabbits (*Oryctolagus cuniculus*) in Scotland are frequently infected with two species of gastrointestinal nematodes (*Graphidium strigosum* and *Trichostrongylus retortaeformis*). Counts of *T. retortaeformis* varied widely between years, whereas those of *G.*

strigosum gradually increased with time. This is because the presence of *T. retortaeformis* elicited an immune response in the host, unlike *G. strigosum* (Cattadori et al., 2007). Warming temperatures have therefore been implicated in the increase in infection intensities as this aids survival of the nematodes in their free-living stage (Crofton, 1948) as illustrated in figure 1 (Harvell et al., 2009).

Parasites and Flycatchers – an ongoing study

Avian malaria

In the strictest sense, malaria refers to infection by *Plasmodium* parasites. However in the field of avian parasite biology, the term is expanded to include *Haemoproteus* and *Leucocytozoon* parasites (Atkinson & van Riper III, 1991). These three genera are closely related Apicomplexan protists in the family Haemosporida. All three genera require two hosts in their life-cycle; a vertebrate host and an insect host, or vector. Haemosporidians have been found in almost all terrestrial vertebrate groups while competent vectors have been found in numerous insect clades. The most important families of these are Ceratopogonidae, Hippoboscidae, Simuliidae and Culicidae. Simuliidae blackflies are important vectors for *Leucocytozoon* and Culicidae mosquitos are the main vectors of *Plasmodium*. *Haemoproteus* is widespread among Hippoboscid louse flies and *Culicoides* midges.

Haemoproteus has a complex lifecycle that involves two hosts, an insect vector and a vertebrate host, most commonly avian or reptilian hosts, but it has also been detected in amphibians (Davies & Johnston, 2000; Engström et al., 2000). The infective stage is the sporozoite which is present in the salivary glands of the insect vector. Once the vector bites a new host, the sporozoites enter the blood stream and invade endothelial cells of blood vessels within various tissues including those of the lung, liver and spleen. Within the endothelial cells, the sporozoites undergo asexual reproduction becoming schizonts. These in turn produce merozoites which attack red blood cells and mature into either female macrogametocytes or male microgametocytes. These two gametocytes can then be ingested by another blood-sucking insect where they undergo sexual reproduction in the midgut of the insect to produce oocysts. The oocysts rupture and release numerous sporozoites that invade the salivary gland and serve as a focus of subsequent infection for another host once the insect takes its next blood meal; thereby continuing the cycle (Fallis & Bennett, 1961; Hall et al., 2005).

Ascertaining which vectors are competent carriers of malaria can be difficult, as presence of the strain does not necessarily mean that it is able to complete its life-cycle. Presence of sporozoites in the salivary glands is usually the best indication (Touray et al., 1992; Kimura et al., 2010; Njabo et

al., 2011). Due to these difficulties, few studies have successfully linked strains to vectors. Currently, none of the strains that have been found in *Ficedula* have been matched to competent vectors. However, there are at least 34 known *Culicoides* species in Sweden (Pettersson et al., 2013), of which at least 17 are known to be ornithophilic; 9, exclusively so. A summary of vector species, feeding preferences and strains can be found in table 1.

Table 1. *Culicoides* species known from Sweden, taken from Pettersson et al., 2013. For feeding preference, O= Ornithophilic; M=Mammalophilic; U= Unknown. Strains and morphospecies taken from the MalAvi database (Bensch et al., 2009).

Species	Feeding Preference	Malaria strain	Morphospecies
<i>C. achrayi</i>	M		
<i>C. albicans</i>	U		
<i>C. chiopterus</i>	MO		
<i>C. circumscriptus</i>	O	BLUTI09; CIRCUM01; CIRCUM02; CIRCUM03; CIRCUM05; CULCIR01; GAGLA03; HAWF2	<i>H. noctuae</i> ; <i>H. concavocentralis</i>
<i>C. clastrieri</i>	MO		
<i>C. comosioculatus</i>	U		
<i>C. deltus</i>	M		
<i>C. dewulfi</i>	M		
<i>C. duddingstoni</i>	O		
<i>C. fascipennis</i>	M		
<i>C. festivipennis</i>	O	TURDUS2	<i>H. minutus</i>
<i>C. grisescens</i>	M		
<i>C. helveticus</i>	U		
<i>C. impunctatus</i>	MO		
<i>C. kibunensis</i>	O	CUK11; CULKIB01; SYAT01; TUPHI01; TURDUS2;	<i>H. syrnii</i> ; <i>H. parabelopolskyi</i> ; <i>H. minutus</i>
<i>C. lupicaris</i>	M		
<i>C. manchuriensis</i>	U		
<i>C. newsteadi</i>	MO		
<i>C. obsoletus</i>	MO		
<i>C. pallidicornis</i>	M		
<i>C. pictipennis</i>	MO	TUPHI01; TURDUS2	<i>H. minutus</i>
<i>C. poperinghensis</i>	M		
<i>C. pulicarus</i>	M		
<i>C. punctatus</i>	M		
<i>C. reconditus</i>	O		
<i>C. riethi</i>	M		
<i>C. salinarius</i>	O		
<i>C. scoticus</i>	MO	CULSCO01	
<i>C. segnis</i>	O	CCF4; CUK11; ROF1; TUPHI01	<i>H. magnus</i> ; <i>H. minutus</i>
<i>C. sphagnumensis</i>	O		
<i>C. stigma</i>	M		
<i>C. subfasciipennis</i>	M		
<i>C. truncorum</i>	O		
<i>C. vexans</i>	MO		

Haemosporidian taxonomy has been a confused area over the years. This is partly due to sampling technique. Older studies that used visual identification described species by appearance (morphospecies), while more modern genetic tools have revealed much higher levels of diversity in these parasites (Cox, 2010; Valkiūnas et al., 2014). Few studies use both techniques in tandem, so many strains are not assigned to a morphospecies and vice versa. Typically a strain is defined as novel if it differs by one base-pair in the mitochondrial cytochrome-b gene (Bensch et al., 2004; Waldenström et al., 2004). This discordance between the two categories has led to some discussion in the field as to the relevance of molecularly identified strains in ecological research (Outlaw & Ricklefs, 2014), especially given the rapid mutation rates or even speciation events within a host (Pérez-Tris et al., 2007). Many of these problems can be solved by using phylogeny to assess the likely impacts of strain relatedness and effects on the host. However, until both the understanding and implementation of molecular methods improve to solve other issues such as reduced dual-infection detection, visual inspection of samples will remain as a valid tool (Valkiūnas et al., 2006; Perkins, 2014).

Ficedula Flycatchers

Collared and pied flycatchers (*Ficedula albicollis* & *F. hypoleuca*) are closely related passerine birds. Both species occur on the Swedish island of Öland. Collared flycatchers are recent colonists to the island and the populations on Öland and Gotland in the Baltic Sea are disjunct from their core range to the south in Central and Eastern Europe. Both species prefer to breed in the same habitats and use the same food resources, however, the more aggressive collared flycatchers competitively exclude pied flycatchers from higher quality, deciduous woodland to lower quality mixed or coniferous woodland (Vallin et al., 2012; Rybinski, 2016). In addition, haemosporidian parasites in this system have been widely studied in the past with 27 different strains detected so far (Wiley et al., 2009; Kulma et al., 2013; Kulma et al., 2014). However, some strains are present in some species more frequently than others, and several strains are only found in one species. Details of strain occurrences and frequencies can be found in table 2; a full description of each strain can be found in the appendix. Variation in habitat types has been shown to lead to different frequencies and diversities of malaria parasites within the same species. For example, Lachish et al. (2011) found that two species of *Plasmodium* had very different transmission rates depending on the microhabitat. For example, *P. circumflexum* transmission was highly correlated with proximity to a water source, whereas *P. relictum* had no such pattern. They suggest that this is down to transmission by different vectors.

Table 2. Haemosporidian strains in their prevalences in *Ficedula* flycatchers on Öland. Information on strain morphospecies and transmission location taken from the MalAvi database. Transmission location refers to the location in the breeding and wintering distribution of pied or collared flycatchers. It should be noted that several of these strains (e.g. SGS1) have been described from a number of locations outside of Europe or Africa. Transmission location is ascertained by the prevalence of each strain in heterospecific species. If a strain has been detected in resident species in both Africa and Europe then it can be assumed to be transmitted on both continents. Modified and updated from Kulma et al., 2013.

Genus	Strain	Morphospecies	Transmission location	Collared Flycatcher	Pied Flycatcher	Hybrid
Haemoproteus	COLL2	<i>H. pallidus</i>	Africa	9.4 (30)	11.5 (14)	0 (0)
Haemoproteus	COLL3	<i>H. balmorali</i>		4.7 (15)	0.8 (1)	0 (0)
Haemoproteus	PFC1	<i>H. pallidus</i>	Europe	2.8 (9)	39.3 (48)	28.6 (4)
Haemoproteus	PHSIB1	<i>H. majoris</i>	Europe	68.7 (219)	38.5 (47)	50.0 (7)
Haemoproteus	WW2	<i>H. majoris</i>	Europe/Africa	0.3 (1)	0 (0)	0 (0)
Plasmodium	ACCTAC01		Africa	0.6 (2)	0.8 (1)	0 (0)
Plasmodium	AEMO01		Africa	0.3 (1)	0 (0)	0 (0)
Plasmodium	COLL10			0.9 (3)	0 (0)	0 (0)
Plasmodium	COLL4	<i>P. homocircumflexum</i>		0.9 (3)	0 (0)	0 (0)
Plasmodium	COLL6	<i>P. delichoni</i>		0.6 (2)	0 (0)	0 (0)
Plasmodium	COLL7		Africa	1.3 (4)	0 (0)	0 (0)
Plasmodium	GRW07			0.3 (1)	0 (0)	0 (0)
Plasmodium	GRW09		Africa	0.6 (2)	0.8 (1)	0 (0)
Plasmodium	GRW10			0.3 (1)	0 (0)	0 (0)
Plasmodium	GRW11	<i>P. relictum</i>	Europe/Africa	0.3 (1)	0 (0)	0 (0)
Plasmodium	LAMPUR03		Africa	0.6 (2)	0 (0)	7.1 (1)
Plasmodium	LBPIP1		Africa	0 (0)	0.8 (1)	0 (0)
Plasmodium	PBPIP1		Africa	0.3 (1)	0 (0)	0 (0)
Plasmodium	PSB1			0 (0)	0 (0)	7.1 (1)
Plasmodium	LINOLI01		Africa	0 (0)	0.8 (1)	0 (0)
Plasmodium	RTSR1		Africa	1.9 (6)	0.8 (1)	0 (0)
Plasmodium	SGS1	<i>P. relictum</i>	Europe/Africa	1.6 (5)	3.3 (4)	7.1 (1)
Plasmodium	SYBOR10		Africa	1.3 (4)	0.8 (1)	0 (0)
Plasmodium	SYBOR05			0.3 (1)	0 (0)	0 (0)
Plasmodium	TERUF02		Africa	0.3 (1)	0 (0)	0 (0)
Plasmodium	TURDUS1	<i>P. circumflexum</i>	Europe/Africa	0.6 (2)	0.8 (1)	0 (0)
Plasmodium	WW4			0.9 (3)	0.8 (1)	0 (0)
Total Infected:				319	122	14

However, the inability for collared flycatchers to completely exclude pied flycatchers from many sites could be driven by parasites. Schall (1992) showed such a relationship with two anole lizards on St. Maartin, in the Caribbean. Both species occupy similar niches and are strongly competitive. *Anolis gingivinus* occupied all areas of the island, whereas the less competitive *A. watsi* is confined to the upland areas in the centre of the island. *P. azurophilum* was found to be a common parasite of *A. gingivinus*, but very rare in *A. watsi*, however the parasite had an uneven distribution across the island. The study showed that both species only co-occurred in the presence of

Plasmodium, when it was absent *A. gingivinus* outcompeted *A. wattsi*. This suggests that the strong bias in *P. azurophilum*'s preference for the more competitive species mediates competition between the two species and allows for coexistence. Species such as *Haemoproteus majoris*, which is more common in collared flycatchers, could be mediating the competitive abilities of this species, allowing for coexistence (Kulma et al., 2013).

Previous work in this system has shown that hybrids have intermediate infection rates (Wiley et al., 2009). However, further work is needed to elucidate these patterns which may vary over time and as more modern screening techniques are used (Waldenström et al., 2004). Therefore, this host-parasite system allows us to gain further insight into the role of parasites in the speciation process and to help predict their role in interspecific interactions as global climate change shifts species ranges and brings taxa into secondary contact.

A full list of malaria strains known from Öland, their transmission location, vectors and breadth of heterospecific infection can be found in the appendix (Bensch et al, 2009; Kulma et al, 2013).

Future direction

Co-evolution of host-parasite interactions and host-specialisation and speciation in parasites has been widely studied in the past (Theron & Combes, 1995; Hoberg et al., 2002; Johnson et al., 2003; Garamszegi, 2009) however, there is a clear need for an increased effort to investigate the role of parasites in the speciation process of their hosts. This is eloquently explained in a review by Karvonen and Seehausen (2012) in which they describe three main prerequisites for parasite-mediated divergent selection: 1.) that infections should differ between or within host populations; 2.) that these differences should remain constant over time, thereby maintaining the direction of selection; and 3.) infections should impose fitness costs on hosts that are sufficiently strong to negate fitness costs of other factors. In addition they highlight three, nonexclusive categories of mechanisms of parasite-mediated host speciation, namely: 1.) direct natural selection: e.g. reduced fitness of hybrid individuals or immigrants; 2.) Pleiotrophy: e.g. selection on immune genes that also affect mate choice; and 3.) Ecologically based sexual selection, where reproductive isolation due to parasite-mediated divergent sexual selection. Yet, while there are studies that have shown empirical evidence for some of these requirements, few have gone further. For a full overview of these studies, see Karvonen and Seehausen (2012). Future studies on the role of parasites in the speciation of their hosts need to take into account these factors.

Conclusion

Parasitism and the steps taken by hosts to combat it are one of the most important aspects of ecology and evolutionary biology. Mounting a defence against parasites is costly to hosts and the lengths that both parties go to, to persist are important drivers of evolution and speciation. Environments and habitats are changing at an unprecedented rate due to anthropogenic forces. This not only results in extinctions, but range expansions and contractions which is bringing many closely related species into sympatry and secondary contact. The role of host-parasite interactions in the maintenance of species should therefore be a priority in future research.

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Appendix

Malaria strains on Öland

In total 27 Haemosporidian strains have been encountered on Öland. A summary of their names, morphospecies and transmission location (if known) and prevalences in collared and pied flycatchers and their hybrids can be found in table 2. A detailed description of each can be found below. Information has been taken from the MalAvi database (Bensch et al., 2009).

Haemoproteus

Haemoproteus strains are the most frequently encountered in *Ficedula* flycatchers and are mostly transmitted in Europe. Despite their high prevalence, only 5 strains representing 3 morphospecies have been discovered so far.

COLL2, *H. pallidus*. This is the most global of the *Haemoproteus* strains in this study. So far this strain has been discovered in 4 families and 5 continents. Öland flycatchers probably acquire this strain in Africa as it has yet to be discovered in resident European species. However, its presence on several other continents could point to the possibility of European transmission. This is a moderately common strain in both species.

COLL3, *H. balmorali*. This is a relatively rare and restricted strain. Other than one record in the spotted flycatcher *Muscicapa striata*, this has only been found in pied and collared flycatchers and the closely related Atlas pied flycatcher (*Ficedula speculigera*). Its transmission zone is currently unknown. This strain is more frequent in collared flycatchers.

PFC1, *H. pallidus*. Other than a record in the hawfinch *Coccothraustes coccothraustes*, this strain has also only been detected in pied and collared flycatchers. Transmission likely occurs in Europe. This is the most frequent strain in pied flycatchers but is relatively rare in collareds.

PHSIB1, *H. majoris*. This is the most abundant strain on the island accounting for 69% and 47 % of infections in collared and pied flycatchers respectively. It is also abundant in hybrids. This is a widespread strain that has been discovered in 6 passerine families to date. Transmission is restricted to Europe.

WW2, *H. majoris*. This has only been found in one collared flycatcher in this study, yet this is a widespread strain found in many European passerines and two non-passerines (corncrake *Crex crex* and Eurasian wryneck *Jynx torquilla*). Transmission appears to be restricted to Europe.

Plasmodium

Plasmodium strains account for a relatively small proportion of infections, however their diversity is much higher. Transmission location in many strains is unknown, although it is likely that greater sampling effort will reveal Africa to be the location for most strains. Morphospecies is also only known for a few strains.

ACCTAC01. Despite being a widespread strain, it is rare in flycatchers. Transmission appears to be restricted to Africa and it has been discovered in many species from 6 orders. This is one of the few strains that has been found in a competent vector, the mosquito *Coquillettidia aurites*.

AEMO01. Rare in flycatchers with only one record, in a collared flycatcher. This is also widespread in passerines, with one record from the cinereous vulture (*Aegyptius monachus*) which suggests that transmission could occur in both Africa and Europe.

COLL10. Apparently rare and restricted to collared flycatchers. So far this strain has only been discovered in Öland collared flycatchers.

COLL4, *P. homocircumflexum*. A rare strain, so far restricted to collared flycatchers. This strain has been found in a peculiar range of species and locations. It has been found in several resident species in Uruguay, A trans-American migrant in the USA and two migratory species in Europe.

COLL6, *P. delichoni*. Another rare strain that so far has only been found in two species. The collared flycatcher and the common house martin (*Delichon urbicum*). As both species are migratory, the transmission location is unknown.

COLL7. Rare in collared flycatchers. This strain has been detected in several resident African passerines from 6 different families. The transmission location is therefore assumed to be Africa.

GRW07. So far only detected in one collared flycatcher in this study and in the great reed warbler (*Acrocephalus arundinaceus*). As both species are migratory, the transmission location is unknown.

GRW09. Occurs in a wide range of African passerine species from many families. This is a rare strain in both flycatcher species. Transmission is probably restricted to Africa. 5 vector species are known: *Coquillettidia aurites*, *C. metallica* and *C. pseudoconopas* and *Culex neavei* and *C. guarti*.

GRW10. A rare strain in collared flycatchers that has been found in 5 species and 4 families. Transmission is probably restricted to Africa.

GRW11, *P. relictum*. This strain is rare in collared flycatchers, but is one of the most widespread strains in passerines. It is found in resident species in both Europe and Africa. *Culex pipiens* and *Culex quinquefasciatus* have been found to be competent vectors.

LAMPUR03. Rare. This strain has only been found in collared and hybrid flycatchers on Öland and the purple-headed starling (*Hylospar purpureiceps*). Transmission is probably in Africa.

LBPIP1. Only known from one pied flycatcher and the long-billed pipit (*Anthus similis*).

LINOLI01. Only known from one pied flycatcher from this study. Also found in a range of African passerines and one non passerine, the Cape gannet (*Morus capensis*). Transmission is probably restricted to Africa.

PBPIP1. Only known from one collared flycatcher from this study. This strain appears to be most common in the Motacillidae, having been found in 3 species in that family. It has also been discovered in 2 other passerine families.

PSB1. A rare strain. This has been found in one hybrid flycatcher from this study and two other species the spotted flycatcher and the pygmy sunbird *Anthodiaeta platura*.

RTSR1. One of the more common *Plasmodium* strains in this study, yet it still only accounts for about 2% of infections. This strain has been found in a wide range of species from 5 orders. Transmission is probably restricted to Africa.

SGS1, *P. relictum*. This is the most widespread of all malaria strains, having been found globally and in most avian orders. Despite this, it is relatively rare in this study and has been found in both species and the hybrids. A wide range of mosquito vectors are known from *Culex*, *Culiseta* and *Lutzia*.

SYBOR05. A rare strain known from one collared flycatcher from this study and the garden warbler (*Sylvia borin*). As both species are migratory, the transmission area is unknown.

SYBOR10. This strain has been discovered in both species, 2 other passerine species from two families and one non-passerine, the corncrake. Transmission of probably restricted to Africa.

TERUF02. A rare strain that has been found in the collared flycatcher, the red-bellied paradise flycatcher (*Terpsiphone rufiventer*) and the non-passerine ruff (*Philomachus pugnax*). Transmission is probably restricted to Africa.

TURDUS1, *P. circumflexum*. Another widespread strain that is apparently rare in flycatchers. This strain has been found in 4 orders, although it is most common in passerines. Transmission seems to be widespread across Europe, Asia and Africa. *Culex pipiens* is the only known vector to date.

WW4. Rare in both collared and pied flycatchers. This strain has also been found in passerines from 4 other families. Transmission appears to be restricted to Africa, although it has been found in several European migrants.

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