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The hitchhiker's guide to avian malaria

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The ecological mechanisms underlying the dispersal of parasites are poorly understood, which is of particular concern in view of currently emerging infectious diseases. In a new study, Pérez-Tris and Bensch examined the distribution and prevalence of avian malaria in a migratory bird across Western Europe. They concluded that repeated independent evolution of year-round transmission has enabled some avian malaria lineages to become more widespread, and more prevalent, than lineages that are transmitted only in summer. This study blurs the boundaries of evolutionary ecology, epidemiology and macroecology with great potential for cross-disciplinary research.

Introduction

Endoparasites, by their very nature, move with their hosts. Migratory birds can travel between continents between breeding and non-breeding areas, offering hitch-hiking parasites an opportunity to extend their geographical range, depending on their ability to adapt to new hosts in a novel environment. Birds are often infected with the vector-borne avian malaria parasites, *Plasmodium* and *Haemoproteus*, but the impact of

these protozoans on wild bird populations is largely unknown. Recent molecular work shows them to be a bewilderingly diverse group, with a wide range of potential hosts [1,2]. Depending on the lineage, avian malaria parasites can switch hosts within and between resident and migrant bird species, sometimes between distantly related hosts [2]. Parasites that are transmitted year-round, infecting wintering migrant hosts, can then disperse to breeding grounds and be transmitted among hosts during the summer. The dispersal potential of year-round transmitted parasites is therefore higher than those that are transmitted seasonally [3]. But is higher parasite dispersal potential associated with increased or decreased local prevalence of infection? In spite of attack from modellers approaches [4], the answer remains largely unknown, which gives cause for concern in an increasingly globalized world offering convenient transmission opportunities for zoonotic and human diseases that threaten human health.

Malaria transmission in a migratory bird

In a recent article [3], Javier Pérez-Tris and Staffan Bensch examined the lineages of avian malaria in a partially migratory bird, the blackcap *Sylvia atricapilla* (Figure 1). Blackcaps breed across Europe and migrate in autumn to the regions around the Mediterranean, where birds from across the breeding range join resident, non-migratory blackcaps for the winter [5]. This period of overlapping winter quarters in southern Spain was pivotal to the study: the mild climate allows vector-borne transmission of malaria between geographically separated host breeding populations. By comparing the winter occurrence of specific cytochrome-*b* mtDNA malaria lineages with that in summer at six breeding sites across Europe from Spain to Sweden, the authors distinguished between parasites that are transmitted all year

round from those that are transmitted only in summer. Six lineages were transmitted all year round, 16 only in summer and two only in winter. A phylogenetic analysis of parasite lineages (Figure 2) showed that year-round transmission to blackcaps has evolved independently on several occasions. This study reveals marked differences in transmission strategy among closely related lineages of avian malaria parasites, with some important implications. It supports recent findings that parasite *cyt-b* lineages are evolutionarily independent entities [6] and suggests that the estimates of enormous biodiversity (in the order of 10,000 species) arrived at by mtDNA sequencing [6] are just the tip of the iceberg. There could be a wealth of hidden genetic variation in within and between avian malaria lineages waiting to be uncovered, for example at loci associated with transmission and infectivity.

From evolutionary ecology to macroecology

Pérez-Tris and Bensch then examined the geographical range of parasite lineages with respect to their dispersal potential and found that year-round transmitted lineages had a much greater range. The authors suggest that those lineages capable of year-round transmission will have more generalist transmission requirements, in terms of vectors and environmental conditions. They go on to suggest that generalist parasites are also more likely to invade new breeding areas successfully. Remarkably, the authors also found that year-round transmitted lineages had a higher local prevalence within breeding populations than did those transmitted only in summer. They suggest that the higher dispersal potential of year-round transmitted lineages results in increased immigration to the local parasite population, providing a source of genetic variation to track host genetic resistance that would otherwise be dependent on mutation and recombination [4,7]. The evolutionary advantage afforded to year-

round transmitted parasites in host-parasite coevolutionary arms races might therefore have enabled them to exploit their host more effectively, achieving higher prevalences than do parasites transmitted only in summer.

This positive correlation between the range and abundance of parasite species extends the ecology of avian malaria into macroecology, raising some intriguing questions. Species abundance-range correlations are well known and all but ubiquitous in animals, but unequivocal support for a mechanism remains elusive [8]. Is the relationship found by Pérez-Tris and Bensch best explained in terms of host-parasite coevolution, as the authors suggest? Can the ecological concepts of niche breadth, density-dependent habitat selection and vital rates, or a combination of mechanisms [8,9] prove useful? The principles and processes of macroecology and metapopulation ecology have many applications to the epidemiology and evolutionary ecology of infectious diseases [10], particularly as host species also vary in the extent and patchiness of their distribution and frequently suffer multiple parasite infections [2,11].

Future directions

Most existing host-parasite studies consider a single host-parasite interaction at small spatio-temporal scales, effectively treating the host as a single patch. Examining multispecies assemblages at a macroecological scale presents a logistical and analytical challenge, but represents a crucial step if we are to understand the distribution and transmission of parasites over large geographical areas. Cross-fertilization of theoretical and empirical studies between macroecology and epidemiology should help to determine the relative importance of the ecology of host versus that of the parasite in explaining patterns of species richness and abundance.

One applied aspect of such work concerns the effects of habitat degradation on parasite community ecology [12,13]. How habitat change might influence parasite dispersal and the emergence of infectious diseases remains largely unknown, as environmental degradation can increase or decrease parasite prevalence [12], but few studies consider community-level patterns. Further work is required to understand the influence of anthropogenic habitat and climate change on both host and parasite biodiversity. Predicted changes in temperature and rainfall will influence the vector ecology of avian malaria [14], but how such instabilities in host-parasite interactions will affect evolutionary processes is difficult to predict.

Although the frequency of host switching in endemic avian malaria is unlikely to present an epidemic threat to human health [1], it might provide a useful model for emerging or re-emerging infectious diseases that threaten human health [15].

Coordinated research to develop our understanding of the ecological mechanisms influencing the transmission of wildlife diseases has obvious merits. Pérez-Tris and Bensch make an important step that often marks major advances in ecology – taking questions inspired by modelling approaches into the field. The ubiquity of avian malaria, and the accessibility of their hosts, makes them an attractive model system for the future study of the ecology, evolution and epidemiology of infectious diseases.

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Legends:

Figure 1. Male blackcap *Sylvia atricapilla* © John Watkins; Frank Lane Picture Agency/CORBIS



Figure 2. The phylogeny and transmission strategy of avian malaria in blackcaps. The phylogenetic relationships between 24 lineages of malaria from blackcaps at six locations in Western Europe are shown. (a) Location of sampling locations (wintering and breeding area, blue circle: SSP, southern Spain; breeding areas, open circles: CSP, central Spain; NSP, northern Spain; FRA, France; BEL, Belgium; and SWE, Sweden). (b) Phylogenetic tree with bootstrap support to internal branches (numbers on branches, values <50% not shown). Each parasite lineage is marked with its transmission strategy: summer only (S) in green, winter only (W) in blue or all year round (Y) in red. Lineages below the dotted line are *Plasmodium* spp., those above *Haemoproteus* spp. of avian malaria. Tick boxes indicate the locations in

which each parasite lineage was detected. year-round transmitted lineages are found in more locations than those transmitted in summer only. Reproduced and adapted with permission from [5].

