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Geographic and within-population structure in variable resistance to parasite species and strains in a vertebrate host

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Abstract

Host resistance to parasites and parasite infectivity may be subject to significant genetically determined variation within species. However, relatively little is known of how this variability is structured in natural vertebrate populations and their macroparasites. A laboratory experiment on host susceptibility–parasite infectivity variation in a wildlife host–parasite system (subspecies of the anuran *X. laevis* and their polystome flatworms), including 33 pairwise allopatric and sympatric host–parasite combinations (three parasite geographical isolates × 11 host full-sibling families, $n = 600$), revealed a complex pattern of infection success. Results amongst host sibships from different localities suggested that infection success was subject to a highly significant locality × parasite isolate interaction. Within localities, a highly significant sibship × isolate interaction also occurred in one of two groups of sibships examined. The existence of such interactions suggests a potential for frequency-dependent, Red Queen-like selection. Interaction between locality and isolate was partly due to higher infection levels in sympatric combinations, consistent with a general pattern of host-specific adaptation. However, some allopatric combinations produced unpredictably high infection levels, resulting in very asymmetrical cross-infectivity patterns (where the reciprocal cross-infections produced negligible infection). This phylogeographically structured host–parasite system may, therefore, sometimes generate local parasite strains with high infectivity to allopatric hosts. Secondary contact between populations could thus result in significant, and unequal, transfer of parasites.

Keywords: Geographic variation; Host resistance; Parasite infectivity; Vertebrate; Flatworm; Red Queen

1. Introduction

A number of prevalent theories explain how natural selection by parasites and pathogens could maintain variation in genetically determined host resistance. One is reciprocal genotype-specific, frequency-dependent selection, as required in the Red Queen hypothesis (Van Valen, 1973; Hamilton, 1980). In this scenario, selection exerted by common parasite genotypes favours rare resistant host genotypes. As the resistant host genotypes become more common, they exert a reciprocal selection pressure on the parasite population favouring rare genotypes better adapted to the demographically expanding host genotypes. This may lead to a continual cycling of host and parasite genotype frequencies within the population. A variety of field and experimental studies carried out on invertebrate hosts support the possibility of Red Queen-type dynamics in some systems (e.g. Lively, 1989; Dybdahl and Lively, 1998; Lively and Dybdahl, 2000; Carius et al., 2001; Decaestecker et al., 2003), but not others (e.g. Kraaijeveld and Godfray, 1999; Green et al., 2000; Ferrari et al., 2001). However, little empirical information is available for vertebrates. Crucially, Red Queen-type selection depends on the way variation in genetically determined parasite infectivity and host susceptibility is structured in natural populations. A Red Queen-type selective regime can only occur where variation in host susceptibility shows an interaction (in the statistical sense) with respect to host and parasite genotype (Carius et al., 2001). In this case, differences in susceptibility between different host genotypes change significantly

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in response to different parasite genotypes. It is well established that resistance to helminth infections in mammals may often be under genetic control, and that helminths themselves show genetic variation in infectivity characteristics (Wakelin et al., 2002). However, relatively little is known about the structure of genetically determined susceptibility–infectivity in wildlife vertebrate–helminth associations (Sorci et al., 1997), especially with regard to potential interactions between host and parasite genotype. Furthermore, although theoretical (e.g. Morand et al., 1996; Gandon, 2002) and experimental studies (e.g. Ebert, 1994) suggest that selective interactions between hosts and parasites may generate spatial patterns, very little empirical data are available on geographical susceptibility–infectivity variation in vertebrates and their macroparasites.

The purpose of this study was to investigate geographical and within-population structure in variable host susceptibility–parasite infectivity using the aquatic anuran, *X. laevis* and its polystome flatworms (*Protopolystoma* spp.) as an experimental model. Two hypotheses were tested: (i) that resistance is subject to an interaction between host lineage and parasite strain or species, within host populations (this is a necessary condition for, and supports the feasibility of, frequency-dependent selection); (ii) that non-random patterns of susceptibility–infectivity occur in sympatric and allopatric combinations between phylogeographically divergent host and parasite populations (i.e. either local parasite adaptation and/or high parasite virulence in some allopatric combinations).

2. Materials and methods

2.1. The host–parasite system

Protopolystoma spp. are oviparous polystomatid monogeneans that reach maturity in the host urinary bladder, following a histozoic juvenile developmental phase in the kidneys. Transmission (by swimming larvae) is direct (Tinsley and Owen, 1975). Modal infection intensities for urinary bladder worms in natural host populations are usually low (one to three worms/infected host) and prevalence is often less than 50% (e.g. Jackson et al., 1998; Tinsley, 1995). Experimental infection studies have shown that primary infections with adult parasites are regulated to these low numbers, even at relatively high larval infection pressures (10–50 larvae/host), by postlarval mortality processes (Jackson and Tinsley, 2003a). The host, *X. laevis*, is fully aquatic, occurring predominantly in still-water habitats (Tinsley et al., 1996). It is widespread in sub-Saharan Africa (occurring within locally variable elevational limits) and currently recognised to comprise a series of distinct subspecies. These are fully interfertile, with hybrids undergoing normal meiosis (Müller, 1977; Graf, 1989).

2.2. Experimental design

An experiment was carried out to investigate host susceptibility–parasite infectivity variation in the *Xenopus-Protopolystoma* system. The central variables were: (i) parasite geographic isolates derived from small groups of infections at known localities, and, (ii) families of host full-siblings lab-raised from wild-caught parents taken at known localities. To assess geographical aspects of infectivity–susceptibility, naïve (previously unexposed) host sibships from different localities and of different subspecies were challenged with different parasite geographic isolates in sympatric and allopatric combinations. To assess within-host-population differences in responses to different parasite isolates, replicate sibships from two localities were studied. In total, infection levels following a primary challenge were measured in all possible pairwise combinations between three parasite isolates (1–3) and 11 host sibships (A–K) ($n = 33$).

The origins of host and parasite material used in this study are summarised in Tables 1 and 2. Parasite isolates 1 and 2 were *Protopolystoma xenopodis*. Isolate 3 contained

Table 1
Details of *Xenopus laevis* sibships used in cross-infection experiments

Sibships	Subspecies	Locality	Latitude	Longitude	Crosses[a]
A	*laevis*	Western Cape area, RSA	34 °05′S	18°34′E	CF1×CF2 (Jackson and Tinsley, 2003a–c)
B	*petersii*	Okavango delta, Botswana	18°58′25″S	22°34′26″E	OK88×OK87
C–G	*laevis*	Pretoriuskop, Mpumalanga, RSA	25°10′06″S	31°15′58″E	C. PK25×PK26 D. PK12×PK24 E. PK16×PK45 F. PK4×PK19 G. PK4×PK44
H–K	*victorianus*	Mukono District, Uganda	00°21′48″S	32°41′48″E	H. MK1×MK8 I. MK5×MK12 J. MK19×MK30 K. MK20×MK30

[a] Designations of individual parents.