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The maintenance of hybrids by parasitism in a freshwater snail

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ABSTRACT

Hybrids have often been labelled evolutionary dead-ends due to their lower fertility and viability. However, there is growing awareness that hybridisation between different species may play a constructive role in animal evolution as a means to create variability. Thus, hybridisation and introgression may contribute to adaptive evolution, for example with regards to natural antagonists (parasites, predators, competitors) and adaptation to local environmental conditions. Here we investigated whether parasite intensity contributes to the continuous recreation of hybrids in 74 natural populations of *Melanopsis*, a complex of freshwater snails with three species. We also examined, under laboratory conditions, whether hybrids and their parental taxa differ in their tolerance of low and high temperatures and salinity levels. Infections were consistently less prevalent in males than in females, and lower in snails from deeper habitats. Infection prevalence in hybrids was significantly lower than in the parental taxa. Low hybrid infection rates could not be explained by sediment type, snail density or geographic distribution of the sampling sites. Interestingly, infected hybrid snails did not show signs of parasite-induced gigantism, whereas all parental taxa did. We found that hybrids mostly coped with extreme temperatures and salinity levels as well as their parental taxa did. Taken together, our results suggest that *Melanopsis* hybrids perform better in the presence of parasites and environmental stress. This may explain the widespread and long-term occurrence of *Melanopsis* hybrids as evidenced by paleontological and biogeographic data. Hybridisation may be an adaptive host strategy, reducing infection rates and resisting gigantism.

1. Introduction

There is growing appreciation among biologists that interspecific hybridisation (i.e., crossing between different species) plays a constructive role in animal evolution (Arnold et al., 1999; Seehausen, 2004; Mallet, 2007), and presents a source for genetic variability (Bullini, 1994). Traditionally hybridisation was only considered important in plants, but it is now evident that animal hybridisation is not as rare and unnatural as previously perceived, involving approximately 10% of animal species (Mallet, 2005). Research on how hybrid zones are maintained, the extent of gene exchange between hybrids and parental taxa (i.e., hybrid introgression), and which selective forces shape hybrid fitness, have made important contributions to our understanding of animal hybridisation (Barton and Hewitt, 1985; Arnold and Hodges, 1995; Fritz et al., 1999). These studies focused mostly on abiotic factors, while biotic factors such as natural antagonists are less often considered (e.g., parasitism, Fritz et al., 1999; Moulia, 1999).

Arms races between natural enemies such as hosts and parasites can lead to high degrees of adaptation and specialisation, and the rapid evolution of extreme traits. It has been suggested that Red Queen dynamics also operate between groups of genotypes belonging to host parental taxa and their hybrids (Wolinska et al., 2008). Although parasite-mediated selection has the potential to maintain the stability of the hybrid zone, by differentially impacting the fitness of host parental taxa and their hybrids (Coustau et al., 1991; Jackson and Tinsley, 2003; Parris, 2004; Wolinska et al., 2006; Batista et al., 2009), direct evidence of such data from natural populations is relatively rare and, more importantly, the reported outcomes are diverse (i.e., in some studies hybrids were more resistant than their parental taxa, whereas in other studies they were more susceptible). One practical reason for the scarcity of field work is the need to sample a sufficiently large number of individuals that are representative of a geographically diverse hybrid zone. This is especially important as the spatiotemporal heterogeneity of parasite load is expected to be highly stochastic (Baird et al., 2012), or if parasites tend to be aggregated within a few hosts, which would result in a right-skewed load distribution with a long tail (Shaw and Dobson, 1995). The sampling methodology employed potentially poses another concern. For

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example, in animals captured using traps (e.g., mice, mosquitoes), parasites may alter host behaviour in that infected hosts are more likely to enter traps (Webster et al., 1994; Irish et al., 2012). This can result in an overestimation of parasite load.

Our current understanding of host-parasite interactions and their potential coevolution in hybrid zones is largely based on observational studies (reviewed in Fritz et al., 1999; Wolinska et al., 2008). One well-studied system is the *Daphnia galeata/hyaline/cucullata* hybrid complex, in which a single lake was sampled over a period of 3 years. Initially, naturally occurring hybrids were frequently infected, whereas parental *D. galeata* were not parasitised (Wolinska et al., 2004). This pattern, however, was reversed as parental *D. galeata* became over-infected within 2 years (Wolinska et al., 2006). Another well-studied hybrid complex involves two subspecies of the house mouse, *Mus musculus musculus* and *Mus musculus domesticus*, where a spatial field study found that hybrids have significantly reduced parasite diversity (Baird et al., 2012). Another field study of a hybrid zone between collared *Ficedula albicollis* and pied flycatchers, *Ficedula hypoleuca*, found that F1 hybrids exhibited prevalences of parasitism and immune responses that were intermediate between the two parental species (Wiley et al., 2009). Taken together, the diversity of outcomes emphasises the need to establish additional hybrid host-parasite study systems. Here we use the freshwater snail *Melanopsis* hybrid complex as a model system for studying snail-trematode interactions. *Melanopsis* has well-defined morphologically distinct species and hybrid forms, and the existence of recent and fossil *Melanopsis* hybrids in the same geographic region suggests a long-term hybridisation history (Heller and Sivan, 2002). Therefore, this complex presents a rare opportunity for investigating the proximate and ultimate factors contributing to our understanding of the factor maintaining hybrids in natural populations.

Melanopsis Férussac 1807 (Gastropoda: Cerithioidea: Melanopsidae) is the most abundant freshwater snail genus in Israel (Heller and Abotbol, 1997; Heller et al., 2005) and is widely distributed in southern Europe, Turkey and northern Africa (Schütt and Bilgin, 1974; Tchernov, 1975; Bănărescu, 1991; Glaubrecht, 1993). Species of the genus *Melanopsis* only reproduce sexually by internal fertilisation (Heller, 2009). The shell structure and texture of species within the genus *Melanopsis* varies considerably (Glaubrecht, 1993; Heller et al., 2005; Heller, 2009), and can be roundish or elongated, smooth or ribbed (Fig. 1). Intermediate forms, whose shells appear half ribbed-half smooth, can be found separately or together with some of the well-defined populations. These observations led Heller and others to describe three *Melanopsis* parental species and hybrid forms (Heller et al., 1999, 2002, 2005). Comparative studies of sperm and radula morphologies, as well as the analysis of allozymes, gave further support for this placement (Hodgson and Heller, 1997; Falniowski et al., 2002; Mazan-Mamczarz et al., 2002).

The aim of this study was twofold. First, we wanted to investigate the role of parasitism in the continuous recreation of hybrids in the freshwater snail *Melanopsis*. To ensure that variation in infection prevalence is driven by hybridisation, and not by differences in snail sex ratios, shell size or abiotic factors such as the type of sediment or the depth of the water in which the different snail species reside, we entered these explanatory variables into our regression model. Second, we tested a competing hypothesis that hybridisation is not driven by parasitism, but instead maintained by differential tolerance to environmental stress. More specifically, we wanted to determine whether *Melanopsis* hybrids tolerate low/high temperatures and salinity levels better than their parental taxa, and whether this tolerance is traded off against resistance to parasites. It should be emphasised that these two hypotheses are not necessarily mutually exclusive, that is, hybrids can be both less parasitised and more tolerant to environmental stress, and vice-versa. To this end we surveyed 74 natural populations of the *Melanopsis* snail complex in Israel, and recorded trematode prevalences and various abiotic parameters. In the laboratory we performed an experiment to examine the influence of low and high temperatures and salinity levels on survival of *Melanopsis* parental species and hybrids.

2. Materials and methods

2.1. Host-parasite system

Melanopsis occur in a variety of water sources and can be found in desert habitats as well as in winter snow areas, and in altitudes that range from 400 m below sea level to 1000 m above sea level. It has a preference for rock dwelling at water surface level, in places where the water current is slow. It is a generalist feeder consuming leaves of higher plants, green algae and cyanobacteria (Mouahid et al., 1996; Heller, 2009).

Melanopsis serves as the first intermediate host of several trematode species (Ismail and Bdair, 1989; Osikovski et al., 1990; Ataev and Dobrovolskij, 1992; Mouahid et al., 1996; Farahnak et al., 2006; Bdir and Adwan, 2011, 2012). In Israel, *Melanopsis costata* was found to be infected by the trematode *Pygidiopsis genata* (Dzikowski et al., 2003) and *Melanopsis saulcyi* individuals, recently collected from Beit She'an Valley, were found to be infected by an as yet unidentified trematode (F. Ben-Ami, unpublished data). Prevalence of infection (by unidentified trematodes) in *Melanopsis buccinoidea* in Israel ranged from less than 10% to over 20% in three

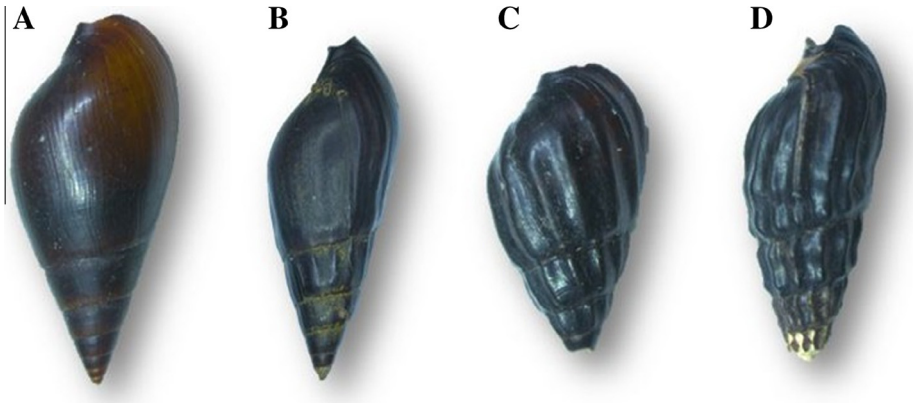

Fig. 1. Recent specimens of freshwater snail genus *Melanopsis* showing shell structure and texture. (A) *Melanopsis buccinoidea*, (B) *Melanopsis costata*, (C) *Melanopsis saulcyi*, and (D) hybrid form.