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Analysis of trait mean and variability versus temperature in trematode cercariae: is there scope for adaptation to global warming?

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The potential of species for evolutionary adaptation in the context of global climate change has recently come under scrutiny. Estimates of phenotypic variation in biological traits may prove valuable for identifying species, or groups of species, with greater or lower potential for evolutionary adaptation, as this variation, when heritable, represents the basis for natural selection. Assuming that measures of trait variability reflect the evolutionary potential of these traits, we conducted an analysis across trematode species to determine the potential of these parasites as a group to adapt to increasing temperatures. Firstly, we assessed how the mean number of infective stages (cercariae) emerging from infected snail hosts as well as the survival and infectivity of cercariae are related to temperature. Secondly and importantly in the context of evolutionary potential, we assessed how coefficients of variation for these traits are related to temperature, in both cases controlling for other factors such as habitat, acclimatisation, latitude and type of target host. With increasing temperature, an optimum curve was found for mean output and mean infectivity, and a linear decrease for survival of cercariae. For coefficients of variation, temperature was only an important predictor in the case of cercarial output, where results indicated that there is, however, no evidence for limited trait variation at the higher temperature range. No directional trend was found for either variation of survival or infectivity. These results, characterising general patterns among trematodes, suggest that all three traits considered may have potential to change through adaptive evolution.

1. Introduction

Species are being exposed to unprecedented rates and combinations of changes in environmental conditions (Vitousek et al., 1997; IPCC, 2007), to which a multitude of responses have already been documented (Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003; Parmesan, 2006). For example, natural populations are responding by shifting their geographic distributions or the timing of growth and reproduction, which due to differential sensitivity among species are bound to affect species interactions, including those between parasites and their hosts (Marcogliese, 2001; Harvell et al., 2002). Populations may also respond to environmental changes through phenotypic plasticity and/or undergo evolutionary adaptation through genetic changes (Bradshaw and Holzapfel, 2006; Gienapp et al., 2008; Hoffmann and Sgro, 2011; Donnelly et al., 2012). The influence of evolution on patterns of biological responses depends on the rate of evolutionary changes as well as the rate of environmental changes (Skelly and Freidenburg, 2010). Of crucial importance for adaptive evolutionary changes to occur is not only the generation time of a particular species, but also the degree of existing variation in critical traits (Houle, 1992; Skelly and Freidenburg, 2010).

High levels of variation for biological traits are common among individuals of the same population (e.g. Marras et al., 2010; Pistevos et al., 2011). This variability is a major determinant of physiological, ecological and behavioural diversity (Aldrich, 1989; Spicer and Gaston, 1999). When heritable, it represents the basis for natural selection processes occurring at the population or species level (Endler, 1986). Phenotypic variability is particularly important in enabling adaptation to changing conditions via natural selection without requiring mutational novelties, in particular when considering that mutational rates in metazoans are usually low (Huey et al., 1991; Hoffmann et al., 2003) and that the rates of on-going environmental changes are unnaturally high (IPCC, 2007). Even if reflecting non-adaptive cryptic genetic variation, phenotypic plasticity in response to altered conditions increases the variance in trait values and may thus facilitate adaptive evolution (Ghalambor et al., 2007).

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Concerns about the potential consequences of global changes for species have led to increased scientific interest in evolutionary adaptive potential and inter-individual variability (see reviews by e.g. Gienapp et al., 2008; Visser, 2008; Skelly and Freidenburg, 2010; Hoffmann and Sgro, 2011; Donnelly et al., 2012). Intra-specific variation has also been investigated in metazoan parasites such as trematodes. For example, intra-specific variation in emergence patterns of trematode transmission stages, i.e. cercariae, has been shown in *Schistosoma* spp. (Ngoran et al., 1997; Theron et al., 1997). Koehler et al. (2011) demonstrated that clones of the intertidal trematode *Maritrema novaezealandensis* have significantly different levels of phenotypic variability in terms of morphology, behaviour and survival (i.e. variability differed across different clones). It was also found that clones of *M. novaezealandensis* showed different levels of host specificity with regards to their ability to infect hosts or develop within them (Koehler et al., 2012a). In the context of climate change and increasing temperatures, Koprivnikar and Poulin (2009) demonstrated experimentally inter- and intra-specific variation in the emergence of intertidal cercariae from infected first intermediate snail hosts at different temperatures. For *M. novaezealandensis*, recent work has shown genotypic differences in cercarial output from snail hosts, pointing toward temperature-clone-specific responses (Berkhout et al., unpublished data). Moreover, in a comparative analysis across several trematode species from a range of systems, inter- and intraspecific variation in responses of cercariae in relation to temperature was found to be common (Morley, 2011; Morley and Lewis, 2013).

As a straightforward index to anticipate the impacts of global change on a wide range of species, estimates of phenotypic variation may prove valuable for identifying species with greater or lower potential for evolutionary adaptation (Chown et al., 2009; Sunday et al., 2011). This should also be the case for parasites and pathogens. Usually, researchers are interested in mean responses and therefore variation in responses is often considered as noise (but see e.g. Aldrich, 1989; Chown et al., 2009; Pistevos et al., 2011; Sunday et al., 2011). However, while experimental error is probably responsible for some of that variation, some of it must be due to genetic differences among individuals (Sunday et al., 2011). Hence, these differences may reveal the "raw material" for natural selection (e.g. Whitehead and Crawford, 2006) and indicate the potential for evolutionary adaptation. This information, provided in published studies as measures of variability (e.g. S.E, S.D.), may therefore be used as an indicator of the scope for evolutionary adaptation.

Here, using the infective stage of trematodes that emerges from first intermediate hosts to infect second intermediate hosts, namely cercariae, we searched the literature to assess means and levels of variability in responses of cercariae to temperature. Cercariae are short-lived, non-feeding transmission stages which are directly exposed to environmental conditions during their search for a host (e.g. Pietrock and Marcogliese, 2003). This stage is a crucial step in the complex life cycle of trematodes. Trematodes typically rely on several hosts plus free-living stages to complete one generation; a fact that may make them particularly vulnerable to loss of species, changing species ranges, or altered environmental conditions directly affecting the parasite (Marcogliese, 2001).

Cercariae are produced asexually within first intermediate mollusc hosts (by intramolluscan stages, i.e. rediae or sporocysts) before leaving the host when conditions are suitable for transmission to the next host. Temperature has been shown to be an important factor affecting the production (i.e. development), emergence and functional aspects (i.e. survival and infectivity) of cercariae. In general, the number emerging is positively related to temperature up to an optimum range (Poulin, 2006; Morley and Lewis, 2013). The survival of cercariae generally decreases with increasing temperatures due to higher activity levels and the faster depletion of their limited energy reserves (Pechenik and Fried, 1995). Infectivity (the percentage of cercariae successfully infecting a host) usually also follows an optimum curve (e.g. Thieltges and Rick, 2006). However, trematodes are a diverse group of species occurring in different habitats and using different hosts to complete their life cycles and hence there are intra- and interspecific differences, e.g. for emergence of cercariae (Morley and Lewis, 2013) as well as for cercarial survival and metabolism (Morley, 2011), making the overall relationship between trematodes and temperature highly complex. Morley and Lewis (2013) also highlighted the importance of incorporating the latitude and acclimatisation regime of organisms into comparative studies of the thermal biology of trematodes, as temperature can have complex effects, especially on cercarial development and emergence, which depend on specific temperature ranges, latitude and the degree of acclimatisation to experimental conditions. While previous studies across trematode species from different systems (but see also Thieltges et al., 2008 for an assessment of cercarial emergence across marine species) analysed mean responses to temperature as Q10 values (i.e. a measure of the change in physiological rates per 10 °C increase in temperature) (Poulin, 2006; Morley, 2011; Morley and Lewis, 2013), the present study is concerned with the original data from the literature, in terms of the mean response, but importantly and as a novel approach, also in terms of the variability in those responses.

Our aim was to assess the mean and the variability of output, survival and infectivity of trematode cercariae (i.e. the expressed, phenotypic variability in those key traits) in relation to temperature, taking a range of factors into account including experimental acclimatisation, latitude, habitat and target host, and using General Linear Mixed Effect Models to analyse the data. For the means of the three response variables, we hypothesised cercarial emergence and infectivity data to follow an optimum curve, and survival of cercariae to decrease with increasing temperature. For the variability of responses, however, several outcomes were possible: (i) variability may increase with increasing temperatures, in particular for cercarial output and infectivity, possibly reflecting the potential for adaptation of trematodes to global warming; (ii) variability may decrease with increasing temperature, especially in the case of cercarial survival, suggesting that trematode parasites may only have limited ability to adapt to increasing temperatures, at least at this stage of their life cycle; (iii) variability may show no significant pattern across the range of temperatures covered, indicating that variability remains unaffected, especially at higher temperature levels. This may also be interpreted as potential scope for adaptation with increasing temperatures. Our study aimed at identifying general patterns that apply to trematodes as a group in order to contribute novel insights into the evolutionary potential of these parasites in the context of global warming.

2. Materials and methods

2.1. Data compilation

Data were obtained from experimental studies of cercarial output, survival and/or infectivity which included at least two temperature levels and which provided S.D.s for response variables (or other measures of variability from which the S.D. could be derived, i.e. S.E.s or confidence intervals (CIs)) (Table 1). The studies were compiled based on an online literature search (scholar.google.com, apps.webofknowledge.com) using several combinations and versions of the terms "cercariae", "trematodes", "output", "emergence", shedding", "production", "survival", "longevity", "infectivity", "infection" and "temperature", as well as by