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Is a jack-of-all-temperatures a master of none? An experimental test with *Daphnia pulicaria* (Crustacea: Cladocera)

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ABSTRACT

A fundamental question in evolutionary ecology is the existence and magnitude of constraints. For example, the proverb 'the jack-of-all-trades is a master of none' refers to one possible constraint, a genetic trade-off of fitness between a generalist and a specialist. It remains an object of controversy. A new method was developed to test experimentally the hypothetical fitness trade-off between a generalist and a specialist that can be used to study populations of both unicellular and multicellular organisms. The method is based on properties of the tolerance curve. The tolerance curve can be defined as the relationship between fitness of a genotype and environmental conditions. Three analytical approaches are possible with respect to tolerance curves: (1) investigation of a genetic trade-off between height and breadth of the tolerance curve; (2) analysis of variance of the area under the tolerance curve among genotypes; and (3) estimation of genetic correlations of fitness on pairs of temperatures. Age of reproduction and clutch size of 29 *Daphnia pulicaria* genotypes from three closely related populations were investigated under seven temperature conditions. Based on these data, fitness – measured as an intrinsic rate of increase (r) – was estimated for each *Daphnia* genotype at seven temperatures. The estimated correlation between height and breadth of the tolerance curve was weakly negative. The analysis of variance of the area under the tolerance curve revealed statistically significant differences among the *Daphnia* clones. The majority of the estimated pairwise genetic correlation coefficients between temperatures were weak, either positive or negative. In general, we observed 'winner' and 'loser' genotypes of *D. pulicaria* in response to temperature, suggesting the need to re-examine the traditional paradigm based on the controversial proverb 'the jack-of-all-trades is a master of none'.

Keywords: *Daphnia*, generalist, niche, specialist, temperature, tolerance, trade-off.

INTRODUCTION

A fundamental question in evolutionary ecology is the existence and magnitude of the constraints described by the familiar proverb 'the jack-of-all-trades is a master of none'.

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The 'jack-of-all-trades' or 'generalist' means an ability to perform under a broad range of conditions; meanwhile, the 'master of none' means poor performance. But what about the 'jack-of-a-few-trades' or 'specialist'? Does it perform better than the 'jack-of-all-trades'? The proverb assumes a genetic fitness trade-off between generality and specialization, and to date it remains an object of controversy (Futuyma and Moreno, 1988; Berenbaum, 1996; Fry, 1996; Reznick *et al.*, 2000).

Three main arguments have been indirectly or directly used in support of the hypothetical genetic fitness trade-off between a generalist and a specialist. First, there is everyday human experience that doing something well is difficult and takes practice so that doing many things well is nearly impossible. Because of this experience, we tend to believe that at some level trade-offs must exist. Second, the trade-off is an application of optimization theory borrowed from engineering and economics and which has been used widely in different fields of biology, including sex ratio theory, foraging theory and life-history theory (Lewontin, 1978; Maynard Smith, 1978; Rose *et al.*, 1987). Usually, optimization models contain an assumption about the constraints that are operating and the optimization criterion that maximizes a quantity of interest. Based on optimization theory, the height of the tolerance curve of an organism is limited by the physico-chemical structures involved, including reproductive constraints and physiological/cellular mechanisms. But the breadth of the tolerance curve cannot be increased without lowering the height – or, in other words, there must exist a value in terms of maximized integrated fitness of a genotype which can also be expressed as an area under the tolerance curve (Levins, 1968). A third argument for the trade-off is based on antagonistic pleiotropy, a genetic mechanism that can be described as allelic effects of opposed direction on fitness. A well-known example of antagonistic pleiotropy is sickle-cell anaemia. Individuals with sickled cells are more resistant to malaria and, therefore, extend their niche breadth into habitat where other individuals may not survive. However, the extension of niche breadth comes with a cost of optimal fitness – that is, anaemia and other side-effects related to the sickled-cell condition. Based on antagonistic pleiotropy, the hypothesis of a fitness trade-off between generality and specialization predicts negative genetic correlations between fitness at optimal and extreme conditions of a single environmental factor.

Multiple theoretical studies dealing with environmental tolerance (Slatkin and Lande, 1976; Lynch and Gabriel, 1987), adaptation to changing environment (Van Tienderen, 1991; Huey and Kingsolver, 1993; Gilchrist, 1995) and breadth of ecological niche (MacArthur and Pianka, 1966; Roughgarden, 1972) have used the 'the jack-of-all-trades is a master of none' assumption to construct models and develop theory. However, empirical evidence for this assumption remains mixed. A variety of studies have dealt with trade-offs in life-history characters (for a summary, see Stearns, 1992; Ross, 1992) and the cost of adaptation to different environments (Dykhuizen and Davies, 1980; Huey and Hertz, 1984; Rausher, 1984; Via, 1984, 1991; Futuyma and Philippi, 1987; James *et al.*, 1988; Pashley, 1988; Karowe, 1990; Robinson *et al.*, 1996; Reboud and Bell, 1997; Keese, 1998; Velicer and Lenski, 1999). Unfortunately, these studies do not provide clear evidence for the existence of a genetic trade-off between height and breadth of the tolerance curve for the following reasons: (1) many of these studies measure how fitness changes over only two or three conditions of a single environmental factor; (2) often some fitness component is measured rather than fitness itself; and (3) studies often make interspecific rather than intraspecific comparisons. In the latter case, results have a limited explanatory power because many properties of specialized species are the consequences rather than the causes of specialization (Futuyma and Moreno, 1988).

Direct experimental tests of ‘the jack-of-all-trades is a master of none’ assumption are few. A powerful way to test this assumption is to examine the fitness of a study organism under a few conditions of a single environmental factor, allow the organism to evolve under extreme conditions, and then re-examine the fitness (Bennett *et al.*, 1992; Bennett and Lenski, 1993; Mongold *et al.*, 1996, 1999; Bronikowski *et al.*, 2001). This approach requires that the model organism has an extremely short generation time to observe a sufficient change in its genetic structure. For example, Bennett *et al.* (1992) and Bennett and Lenski (1993) have used this approach to measure the evolutionary response of *Escherichia coli* to temperature. After maintaining their cultures for 2000 generations, they concluded that declines in performance at non-stressful temperatures were not a necessary consequence of adaptation to the stressful high-temperature regime. But to date this approach has been restricted mainly to unicellular organisms because of their rapid reproduction.

We developed a method to test experimentally the hypothetical fitness trade-off between a generalist and a specialist that can be used to study populations of both unicellular and multicellular organisms. The method is based on three independent analytical approaches. First, to examine the genetic correlation between height and breadth of the tolerance curve. If the assumption about the trade-off is correct, we predict a negative correlation between height and breadth of the tolerance curve. Second, to estimate the area under the tolerance curve and compare it among genotypes. If the assumption about the trade-off is correct, we predict no significant variation of the area under the tolerance curve among genotypes. Third, to calculate the genetic correlations of fitness across different environmental conditions. If the assumption about the trade-off is correct, we predict negative genetic correlations between fitness at optimal and extreme conditions.

The tolerance curve shows the relationship between fitness of a genotype and environmental conditions, and reflects three important characteristics of the genotype’s tolerance to a specific environment: the maximum fitness value under optimal conditions (which is reflected by the height of the tolerance curve), an ability to maintain a non-zero fitness value under the broad range of an environmental factor (which is reflected by the breadth of the tolerance curve), and the total integrated fitness (which is reflected by the area under the tolerance curve).

We used this method to investigate experimentally the possibility of genetic fitness trade-off between a generalist and a specialist regarding adaptation to temperature in *Daphnia pulicaria* (Crustacea: Cladocera). *Daphnia pulicaria* is a freshwater crustacean, distributed in lakes of North America and Europe (Hrbáček, 1987; Černý and Hebert, 1993), and possesses four characteristics important for this study: (1) the ability to reproduce asexually, which allows replication of multiple copies of the same genotype and evaluation of the genotype’s fitness under a range of environmental conditions; (2) a high rate of growth and reproduction, which minimizes the length of experiments, allows a larger scale study and allows a more complete estimate of fitness; (3) ease of maintenance in the laboratory; and (4) extensive background information, which allows synthesis into a larger body of understanding of *Daphnia* ecology, genetics and evolution.

We estimated tolerance curves of 29 *D. pulicaria* genotypes in response to a range of seven temperatures. We chose temperature as an environmental variable because it has a profound effect on the geographical distribution of *Daphnia* species as well as on habitat selection (e.g. lakes versus ponds). Temperature varies both spatially and temporally; natural populations of *Daphnia* are frequently exposed to different temperature regimes, and they can be expected to adapt evolutionarily to characteristic thermal environments.

METHODS AND MATERIALS

Establishment of *Daphnia pulicaria* clones

Daphnia pulicaria individuals were collected from three closely located Wisconsin populations: Mendota Lake, Waubesa Lake and the Yagara River basin. After being transported to the laboratory, each individual was isolated and maintained under favourable conditions to establish clones. Each clone was assessed electrophoretically for four enzymes: PGM (phosphoglucomutase), GPI (glucose-6-phosphate isomerase), AAT (aspartate amino transferase) and LDH (lactate dehydrogenase) (Hebert and Beaton, 1993). In addition to morphological characteristics (Brooks, 1957; Brandlova *et al.*, 1972), LDH was used as a molecular marker to help to distinguish *D. pulicaria* species from morphologically similar *D. pulex* (Hebert *et al.*, 1993). Twenty-nine *D. pulicaria* clones with electrophoretically distinct genotypes were maintained in the laboratory for life-history experiments.

Experimental assessment of survivorship and reproduction

Survivorship and reproduction of 10 replicates of each studied *D. pulicaria* clone were estimated under each of seven temperature conditions: 11°C, 14°C, 17°C, 20°C, 23°C, 26°C and 28°C. Individuals obtained from each clone were randomly positioned in beakers in a controlled light cabinet (12L : 12D). The beaker contained 200 ml of a standard laboratory medium, consisting of filtered pond water and zooplankton media (1 : 1) (Lynch *et al.*, 1986) with green algae *Scenedesmus* added daily (approximately 300,000 $\text{cell}\cdot\text{ml}^{-1}$). To eliminate maternal environmental effects (Lynch and Ennis, 1983), each individual was acclimatized for one generation to the experimental conditions. Two life-history parameters were monitored daily: the age of reproduction and the number of offspring released per clutch. The experiment was concluded when every surviving individual released its fourth clutch of offspring. All temperature conditions were evaluated within a period of 5 months after the collection of each clone.

Estimation of fitness

Using information collected from the experiment, the mean life table for each clone was constructed. When generations overlap, as in *Daphnia*, usually instantaneous rate of increase, r, is calculated instead of net reproductive rate, R (Ricklefs, 1979; Futuyma, 1997). Because our experimental conditions were close to optimal, we used intrinsic rate of increase, r_m (also called the *Malthusian parameter*), to estimate the potential genotype's performance under different temperatures. The theory of population growth (Ricklefs, 1979) states that if a population remains under constant conditions and, therefore, has constant age-specific survival and fecundity for sufficient time (as in our experimental *Daphnia* populations), the growth rate of the population will become constant and the population will assume a stable age distribution. As a result, we used a stable age or Euler-Lotka equation to estimate the instrinsic rate of increase, r_m, of each *Daphnia* genotype under different temperatures.

The intrinsic rate of increase, r_m, which was used as a measure of absolute fitness, was iteratively estimated for each clone by fitting individual values of x, l_x and m_x – where x is age, l_x is survival through age x, and m_x is fecundity at age x – to the stable age or renewal equation (Euler-Lotka equation):

$$\sum l_x m_x e^{-rx} = 1$$

Previous research (e.g. Spitze, 1991) has shown that estimates of age of reproduction and clutch size in *Daphnia* up to the fourth clutch constitute about 90% of the estimated intrinsic rate of increase, r_m, and provide a fairly good estimate of total fitness.

Individuals that did not survive to the first clutch were not replaced. The estimated fitness value of a clone thus reflects three life-history components: age of reproduction, clutch size and juvenile survivorship. Any clone that produced less than 10 offspring at a specific temperature (< 1 offspring per replicate) was assigned a value for r_m of 0.

Statistical analysis

The tolerance curve for each clone in response to temperature was obtained by least squares fit of a quadratic function to the fitness data of the clone (Sokal and Rohlf, 1995). By projecting temperature on a linear scale, different functions may be applied to fit the data: polynomial, modified sigmoid, Logan *et al.* (equation 6) (Logan *et al.*, 1976). By transforming (if necessary) temperature into a non-linear scale, it is possible to fit functions that are symmetrical (e.g. Gaussian or quadratic). We selected a quadratic function because this function allows a straightforward approach to calculating both maximum fitness values and temperatures when the fitness is equal to zero.

Analysis of variance (ANOVA) was performed for the parameters of height, breadth and the area under the tolerance curve of all studied *D. pulicaria* genotypes to ensure that there were no effects attributable to the studied populations.

The genetic trade-off between height and breadth of the fitness curve was tested by using parameters from the quadratic function fit to the fitness data for each clone. These parameters were: x_1, the minimum temperature value with a non-zero r_m; x_2, the maximum temperature value with a non-zero r_m; and y_{max}, the maximum height of the tolerance curve. The difference between x_2 and x_1 represents the breadth of the tolerance curve. After fitting the quadratic function to the data, the estimated values for height and breadth of the tolerance curve for each *D. pulicaria* genotype were used in a standard product–moment correlation analysis. A negative correlation between height and breadth indicates a trade-off, whereas a positive or zero correlation indicates no trade-off.

A necessary prerequisite for the test examining the trade-off between height and breadth of the tolerance curve among different genotypes is the existence of genetic variance for height and breadth. Two tolerance curves per clone were constructed based on average r_m values of five replicates. Then, height and breadth were estimated for each tolerance curve. One-way ANOVA was used to evaluate the genetic differences for height and breadth among the clones.

Differences in the area under the tolerance curve among *D. pulicaria* genotypes were examined in the following way. First, two tolerance curves per clone were constructed based on average r_m values of five replicates. Next, the area under each tolerance curve was estimated by integrating the quadratic function fitted to the fitness data. Differences in the tolerance area among 29 *D. pulicaria* clones were evaluated with one-way ANOVA.

The cross-temperature genetic correlations for fitness (r) were calculated as standard product–moment correlations of clone means (Via, 1991).

RESULTS

A quadratic function fitted well ($R^2 = 89\%$) to the average fitness data across the clones, eliminating the need to transform temperature to a non-linear scale (see Fig. 1). Analysis of variance revealed highly significant ($P < 0.05$) genetic variation for both height and breadth of the tolerance curve (Table 1). These results suggest that within the *D. pulicaria* populations examined there exists a substantial amount of genetic variation that would allow evolution of tolerance curves in response to temperature. No effects were found that were attributable to the studied populations.

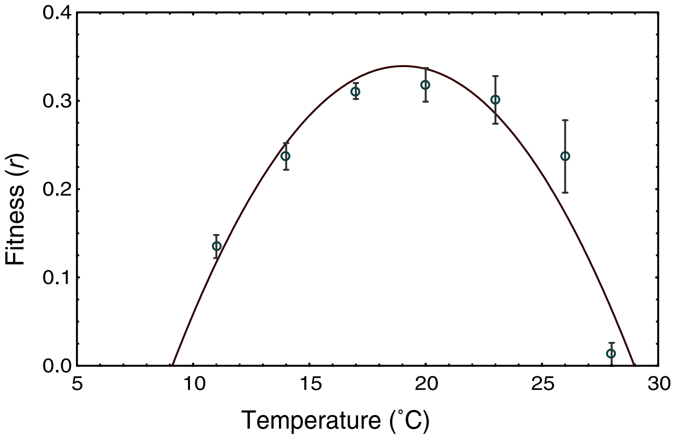

Fig. 1. Best fit quadratic function on average fitness (r_m) of 29 *D. pulicaria* clones in response to seven temperature conditions (± 95% confidence intervals; $R^2 = 0.89$).

Table 1. Results of analysis of variance of breadth and height of quadratic functions fitted on fitness data of 29 *D. pulicaria* clones in response to temperature

Source	SS	d.f.	MS	F	R^2	P
Variation in breadth						
Between genotypes	305.41	28	10.91	3.27	0.53	<0.05
Within genotypes	96.87	29	3.34			
Total	402.28	57				
Variation in height						
Between genotypes	0.132	28	0.0047	4.03	0.63	<0.05
Within genotypes	0.034	29	0.0012			
Total	0.166	57				

Note: One quadratic function was fitted on fitness data based on five replicates of a clone, total two quadratic functions per clone.

The correlation between height and breadth of the tolerance curve was weakly negative ($r = -0.05$) (Fig. 2). The variance in the area under the tolerance curve among *D. pulicaria* clones was highly significant ($P < 0.001$) (Table 2). These results indicate the existence of variability in tolerance area among genotypes that would allow some clones to possess both greater height and greater width than other clones.

Genetic correlations of fitness attained on pairs of temperatures are provided in Table 3. The majority of the estimated correlation coefficients were weak, either positive or negative. A few of them were statistically significant ($P < 0.05$): 0.509* between 14°C and 17°C, 0.511* between 20°C and 23°C, and −0.398* between 17°C and 23°C. There was no apparent relationship in fitness among low, optimal and high temperatures.

DISCUSSION

Experimental estimation of breadth and height of the tolerance curve as well as the area under the tolerance curve, together with the direct estimation of fitness, is probably the most accurate method of measuring degrees of ecological specialization. The ability to distinguish objectively a specialist from a generalist is essential for the test of the genetic fitness trade-off between being a generalist and a specialist. This study is the first attempt to test the hypothetical genetic fitness trade-off between a generalist and a specialist by using

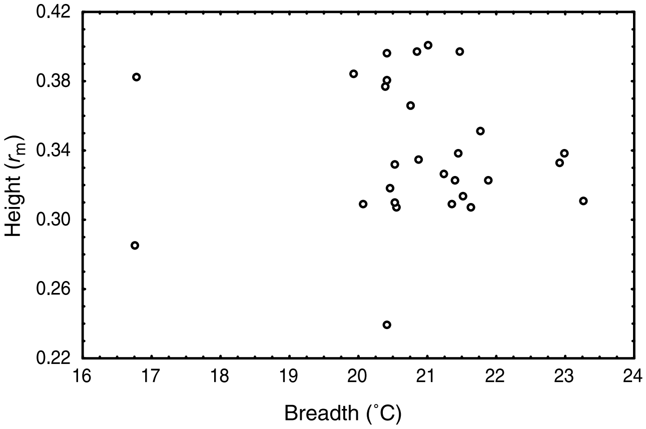

Fig. 2. Correlation between height and breadth of the quadratic functions fitted to the fitness data of 29 *D. pulicaria* clones in response to temperature ($r = -0.05$).

Table 2. Results of analysis of variance of areas under the quadratic functions fitted on fitness data of 29 *D. pulicaria* clones in response to temperature

Source	SS	d.f.	MS	F	R^2	P
Between genotypes	16.87	28	0.602	4.31	0.62	<0.001
Within genotypes	4.06	29	0.140			
Total	20.93	57				

Note: One quadratic function was fitted on fitness data based on five replicates of a clone, total two quadratic functions per clone.

Table 3. Estimates of genetic correlations of fitness (*r*) of *D. pulicaria* attained on pairs of temperatures, calculated as product–moment correlations on clone means

	14°C	17°C	20°C	23°C	26°C
11°C	0.003	−0.015	−0.018	0.217	−0.053
14°C		0.509*	−0.004	−0.279	−0.096
17°C			−0.045	−0.398*	−0.273
20°C				0.511*	0.208
23°C					0.208

* $P < 0.05$.

parameters (height, breadth and the area under the tolerance curve) estimated from the tolerance curve. Our results indicate that the proverb 'jack-of-all-trades is a master of none' cannot be applied in the case of *Daphnia pulicaria* adaptation to temperature. This conclusion was reached by following three independent analytical approaches that provided consistent results.

The first approach was to examine the genetic correlation between height and breadth of the tolerance curve. Our analysis failed to find a negative relationship between these two parameters and it did not support the trade-off hypothesis. Because this is the first experimental study using correlation analysis to test the genetic trade-off between height and breadth of the tolerance curve, we cannot compare our results directly with those of other studies. Bronikowski *et al.* (2001) examined thermal tolerance curves of bacteria *Escherichia coli* and *Salmonella enterica*, and compared the curves from seasonal, geographic and phylogenetic perspectives. However, they did not provide a statistical analysis of the trade-off between height and breadth of the tolerance curve, making their results difficult to evaluate. In another study, Sopina (1976) observed thermal tolerance curves of four strains of *Amoeba proteus* (Protozoa), which showed substantial differences in height of the tolerance curves while maintaining similar breadth. In another study, Bosch *et al.* (1988) found that a freshwater coelenterate, *Hydra attenuata*, was able to survive short-term exposure to high temperature because of the synthesis of a major heat shock protein. They demonstrated that the presence of the heat shock protein did not have any effects on normal growth or physiology of *H. attenuata*.

The second approach to investigating the genetic trade-off between height and breadth of the tolerance curve was by estimating the area under the tolerance curve and comparing it among genotypes. A similar area under the tolerance curve among genotypes would be evidence to support the genetic trade-off, whereas significant variation in the area would suggest the absence of a trade-off. We found statistically significant differences in the tolerance area among the genotypes, which supports our results obtained from the correlation analysis between height and breadth of the tolerance curve. The variation in the tolerance area implies that some *D. pulicaria* clones are fitter than others across temperatures. We were unable to find any comparable results dealing with genetic intraspecific comparison of area under the tolerance curve from other studies. Sopina (1976), Bennett and Lenski (1993) and Bronikowski *et al.* (2001) allowed only visual comparison of the area under the estimated temperature tolerance curves among genotypes, which was not conclusive.

The third approach to evaluating the fitness trade-off between a generalist and a specialist was to calculate the genetic correlations of fitness across different environmental conditions. The hypothesis of a trade-off between height and breadth of the tolerance curve predicts negative genetic correlations between fitness at optimal and extreme temperatures. In this study, genetic correlations of fitness attained at pairs of temperatures showed no general trend. Most correlations were not significant; those that were significant were as likely to be positive as to be negative. The obtained positive and negative correlations within the investigated temperature range suggest the existence of multiple action and probably a compensatory effect of different mechanisms (e.g. protein polymorphism, structure of membranes, stress proteins, etc.) that are responsible for the adaptation to different temperature conditions. In addition to studies discussed earlier (Bennett *et al.*, 1992; Bennett and Lenski, 1993; Mongold *et al.*, 1996, 1999), comparable results were obtained by Futuyma and Philippi (1987), who studied diet specialization in the larva of *Alsophila pometaria* (Lepidoptera). Futuyma and Philippi (1987) estimated genetic correlations of larval weight attained on pairs of four plant hosts, calculated as product–moment correlations on corrected family means. The obtained correlations were mostly weak, and only two were statistically significant: one was negative and the other was positive. Other studies of diet specialization that estimated genetic correlations were based on only two plant hosts, some of which reported negative genetic correlations (Via 1991), some of which reported positive genetic correlations (Rausher, 1984; Via, 1984; Karowe, 1990), while others did not find correlations significantly different from zero (Pashley, 1988; Keese, 1998).

In general, we observed ‘winner’ and ‘loser’ genotypes of *D. pulicaria* in response to temperature or, in other words, some genotypes in nature have both wide thermal breadth and heightened fitness. Thus, evidence from previous experimental studies (e.g. bacteria experimental evolution: Bennett *et al.*, 1992; Bennett and Lenski, 1993; Bronikowski *et al.*, 2001) and now *Daphnia* questions the generality of the fitness trade-off between a generalist and a specialist, also described by the proverb ‘jack-of-all-trades is a master of none’, and suggests the need to re-examine the traditional paradigm. What testable mechanisms could be responsible for the existence of ‘winners’ and ‘losers’ in natural populations? How often do they happen in nature? We think that these questions deserve attention and further experimental investigation.

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