



Heritability of body size matches trait evolution in the range expansion of a biological control agent

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ABSTRACT

Adaptive evolution requires both natural selection and genetic variation. In introduced species, the selective dynamics of range expansion are predicted by theory to lead to differences between the core and the leading edge, with edge individuals evolving to be more fecund (under *r*-selection) and have greater dispersal ability than core individuals. In arthropods, both fecundity and dispersal ability are often positively correlated with body size. Here, we quantify genetic variation available for evolution of body size in a beetle (*Diorhabda carinulata*) introduced into North America as a biological control agent. Previously, we found that females at the edge of the range expansion have evolved to be larger than those at the core as predicted by theory, while male body size has not clearly changed, despite the evolution of increased dispersal capacity. Using a half-sib mating design, we measure genetic variation in mass at eclosion and thorax width of female and male beetles from a single introduced population at the core of the range expansion. We find significant heritable genetic variation in females in both traits, but not in males. Thus, lack of genetic variation in body size may preclude evolution of size in males along this expansion front.

1. Introduction

Evolution requires genetic variation, and genetic variation appears to be abundant in natural populations (Postma 2014; Wood et al., 2016). Indeed, examples of rapid evolution, initially surprising, are now common (Carroll et al. 2007). However, range limits, and other examples of evolutionary stasis provide evidence that constraints to evolution exist, in the form of trade-offs or limited genetic variation (Hoffmann, 2017; Angert et al. 2020). Many examples of rapid evolution stem from introduced species, which are likely to experience novel selection pressures in their new ranges (Reznick and Ghalambor 2001), and which, despite potential founder effects associated with introduction to new ranges, often have sufficient genetic variation to evolve (Estoup

et al. 2016).

One important line of evidence of the evolution of introduced species comes from comparing populations from their initial introduction sites (the core) to the expanding edge of the new range. Individuals at the leading edge may experience selection for higher fecundity (essentially “*r*-selection”) when the expanding edge population is at low density, which favors individuals that produce many offspring (Phillips et al., 2010; Burton et al. 2010). Additionally, range expansion can lead to the evolution of higher dispersal capacity through the process of spatial sorting, where more dispersive individuals reach the edge, leading to assortative mating by dispersal ability (Phillips and Perkins 2019). If there is a genetic basis to dispersal, this then leads to more dispersive offspring.

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In arthropods, evolution in response to such selection along an expansion front may be evident in shifts in body size. Fecundity increases with female body size in most insects (Honěk, 1993), thus if there is selection for higher fecundity at the edge it should also lead to increased size of females at the edge relative to the core (Clark et al. 2022) if there is sufficient genetic variation. The relationship between dispersal capacity and body size is less well studied, but dispersal distance generally increases with mass in ectotherms (Stevens et al. 2014) and has been shown to increase with wingspan in butterflies (Sekar, 2012) and with body size in male ground beetles (Laparie et al. 2013; Yarwood et al., 2021). Thus, spatial selection for dispersal may lead to larger size of both males and females.

Here, we examine genetic variation in body size in a beetle introduced into North America for biological control to understand how the availability of genetic variation may have shaped evolution during this range expansion. Previously, we found that females from the edge of the range expansion have evolved both higher fecundity and larger body size relative to the range core (Clark et al. 2022). Additionally, using flight mills, we found that males from the edge (reared in the lab for a generation to standardize environmental effects) have evolved increased dispersal capacity, but there is no evidence that body size of males has evolved (Clark et al., 2022). Our goal here was thus to quantify genetic variation in body size in both males and females to infer whether the availability of genetic variation might either facilitate or constrain evolutionary shifts. We focus on a single population from the core of the range.

2. Methods

2.1. Study system

The northern tamarisk beetle (*Diorhabda carinulata*: Coleoptera, Chrysomelidae, hereafter the tamarisk beetle or simply the beetle) is a specialist herbivore used for biological control of tamarisk (*Tamarix* spp.), a woody shrub invasive in North America. The beetle was released into the United States in 2001 (DeLoach et al., 2003), and initially established at the 38th parallel and further north, being limited by inappropriate timing of diapause further south (Bean et al. 2012; Clark et al. 2023). However, diapause timing evolved rapidly, allowing subsequent expansion southward.

2.2. Approach

To understand how genetic variation may have impacted range expansion, we measured genetic variation in two morphological traits, body mass and thorax width. We focused on one of the original release sites (Delta, Utah 39.144, -112.958) because genetic data show that this site was likely an origin of the range expansion southward (Stahlke et al. 2022) and genetic variation at the core of the expansion is crucial for evolution during the expansion. Individuals were collected in 2018 by hand and reared in the lab for three to four generations in bulk containers with tamarisk to standardize parental environmental effects. We then used a paternal half-sibling breeding design (Lynch and Walsh 1998) to estimate components of genetic variance in two measures of size: body mass at eclosion and thorax width.

Thirty-nine sires (males) of the second lab generation were each mated to seven or eight dams (females) total. This was done by placing two to three females with one male in a single dish and replacing the females every 48 h, until seven or eight females had been mated with each male. We did not record the number of matings, but many were successful, as 38 sires and between 1 and 8 dams per sire produced offspring for a total of 238 families. Eggs were collected from each dam and reared in full-sibling families. When larvae were 3rd instars, density was standardized to 15 larvae per full-sibling family per 0.24 L container, to reduce environmental variation that might obscure additive genetic variation. When the offspring reached adulthood, we

measured mass at adult emergence (before feeding) and thorax width on two females and one male per full-sibling family. We measured weight for 730 adults, and thorax width for 615 adults.

2.3. Analysis

To understand how genetic variation in morphological traits may have impacted range expansion, we estimated both heritability (h^2) and evolvability (I^A) in the two traits (Houle 1992; Lynch and Walsh 1998; Hansen et al. 2011). Heritability scales additive genetic variation by total phenotypic variation of a trait, while evolvability scales additive genetic variation by the mean value of the trait and is interpreted as the proportion change in a trait over a generation of selection. Heritability has been used historically and provides intuitive values, while evolvability has been suggested to be a better measure of evolutionary potential (Hansen et al. 2011; Houle 1992).

All analyses were separate for males and females, since tamarisk beetle females are generally larger than males (Lewis et al. 2003). Additive genetic variance was estimated as $V_A = 4 \times V_{\text{sire}}$ (as additive genetic variance due to dam cannot be estimated with this breeding design and is assumed to be similar to sire variance) (Lynch and Walsh, 1998). For females, two full siblings were measured per family, allowing us to incorporate random effects of dam into the estimate of total phenotypic variance as $V_P = V_{\text{sire}} + V_{\text{dam(sire)}} + V_{\text{resid}}$ (Lynch and Walsh 1998). For males, total phenotypic variance was estimated as $V_P = V_{\text{sire}} + V_{\text{resid}}$.

Narrow-sense heritability was calculated as $h^2 = V_A/V_P$. Evolvability was calculated as $I_A = V_A/m^2$, where m is the trait mean (Hansen et al., 2011; Houle 1992). Likelihood ratio tests were used to determine the significance of the sire variance component (V_{sire}). Standard error and confidence intervals around V_A , V_P , h^2 , and I_A as well as differences between them were calculated with a bootstrap method, following Houde and Pitcher (2016). Briefly, sires were drawn with replacement up to the original sample size and the variance components, heritability, and evolvability were calculated as above for each sample. 1000 random samples were drawn, and variance, standard error, and confidence intervals were calculated from the resulting distribution.

This approach enables comparison of heritability and evolvability by sex, and also allowed us to examine the correlation between these two estimates of body size. The average weight and thorax width of individual half-sib families was estimated from the model using the RESim function of the merTools package (Knowles and Frederick 2024). All data were analyzed using the statistical software R version 4.2 (R Core Team 2022) and code for the analysis is available in the Supplement. We describe our results using the language proposed by Dushoff et al. (2019) for describing whether or not differences are clear, to avoid use of an arbitrary p-value cut-off.

3. Results

Both phenotypic variance and additive genetic variance in body mass were higher in females than males (Fig. 1A). The sire variance component was marginally significant for males (likelihood ratio=3.55, $df=1$, $P = 0.059$), while for females it was highly significant (likelihood ratio=20.28, $df=1$, $P < 0.000001$). Heritability of body mass was 0.53 (95 % CI 0.11,0.87) for females and 0.31 (95 % CI 0,0.59) for males (Fig. 1B). The confidence interval around the difference in heritability between males and females overlapped zero (difference=0.228, (95 % CI -0.22, 0.71) calculated following Houde and Pitcher (2016) as described in the methods). Variation in female mass among families was substantial (Fig. 1C), with the smallest (raw) family mean being 9.5 mg and the largest being 12.9 mg, 35 % larger than the smallest. This range is similar to what Clark et al. (2022) observed, with mass in core populations from that study varying between 6.5 mg and 12.3 mg. In that study, females from populations at the expanding edge weighed 7 % more than females from core populations. Only the heritability estimate for females was statistically greater than zero. Evolvability of body mass

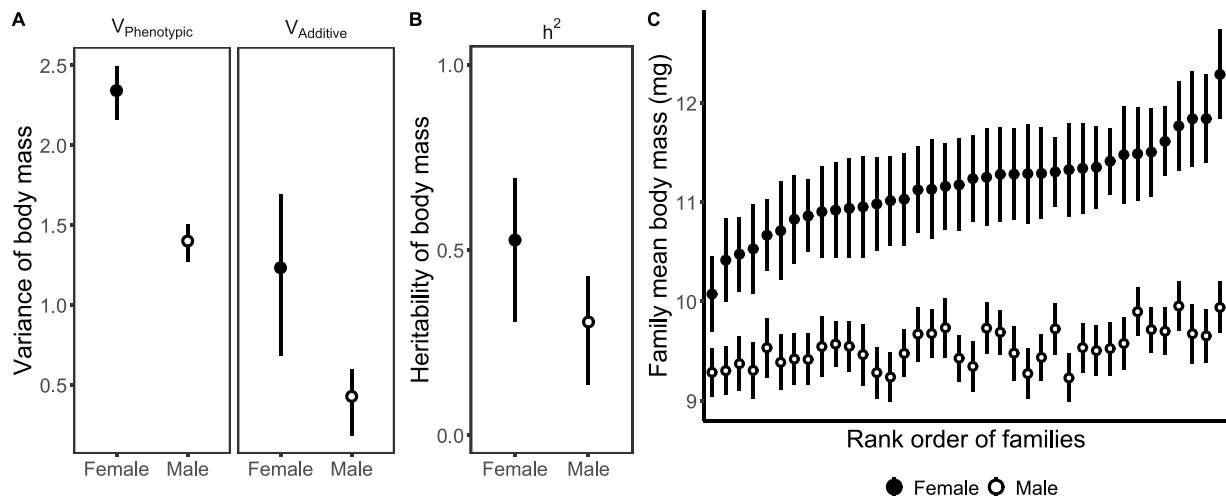


Fig. 1. A. Total phenotypic and additive genetic variation. B. Heritability of body mass at eclosion of males and females (means and SDs). C. Mean body mass for males and females by half-sib family, estimated from the random effects models, ordered on the x-axis by half-sib family mean of body mass for females.

for both males and females were close to zero and not statistically different from zero (Table 1).

The patterns were similar for thorax width, though variance and heritability were smaller. Both phenotypic and additive genetic variance were higher in females than males, leading to a heritability estimate of 0.36 (95 % CI 0.07,0.61) for females and 0.05 (95 % CI 0,0.29) for males (Fig. 2). However, the confidence interval for the difference in heritability between males and females slightly overlapped zero (difference=0.273, 95 % CI -0.01, 0.56). The sire variance component was statistically significant for females (likelihood ratio=8.4198, df=1, $P = 0.003712$), but not for males (likelihood ratio=0.13062, df=1, $P = 0.7178$). Evolvability of thorax width was estimated to be zero for both males and females (Table 1).

Body mass and thorax width are positively and statistically clearly correlated with each other (Pearson correlation=0.64, 95 % CI 0.59, 0.68)), as expected for these two measures of body size.

Discussion

We found heritable variation in body mass and thorax width of female tamarisk beetles, which coincides well with evidence that female body mass increased 7 % at the edge of the tamarisk beetle range expansion (Clark et al., 2022). Interestingly, though often considered a better predictor of evolution, evolvability for both traits was zero.

Table 1
Variance components, heritability, and evolvability for body mass and thorax width of females and males. Standard deviations (SD) estimated from bootstrap procedure.

		V_{Additive}	$V_{\text{Phenotypic}}$	h^2	I_A
Female body mass	Estimate	1.23	2.34	0.53	0.01
	Bootstrap SD	0.51	0.17	0.20	0.00
	Bootstrap 95	(0.23,	(2.03,	(0.11,	(0.00,
	% CI	2.25)	2.66)	0.87)	0.02)
Male body mass	Estimate	0.43	1.40	0.31	0.00
	Bootstrap SD	0.21	0.12	0.15	0.00
	Bootstrap 95	(0, 0.82)	(1.16,	(0, 0.59)	(0, 0.01)
	% CI		1.64)		
Female thorax width	Estimate	0.01	0.03	0.36	0.00
	Bootstrap SD	0.00	0.00	0.14	0.00
	Bootstrap 95	(0, 0.02)	(0.02,	(0.07,	(0, 0)
	% CI		0.03)	0.61)	
Male thorax width	Estimate	0.00	0.02	0.05	0.00
	Bootstrap SD	0.00	0.00	0.09	0.00
	Bootstrap 95	(0, 0.01)	(0.02,	(0, 0.29)	(0, 0)
	% CI		0.03)		

Clearly, however, female body size was able to evolve (Clark et al., 2022), suggesting that in this case, heritability is more predictive of evolution given selection. Given how much family level variation in female mass is evident in this core population (with the largest families weighing 35 % more than the smallest), it appears that there is room for yet larger body size to evolve at the expansion front, if selected for. The observation that the body size of females in edge populations has not continued to increase given ample genetic variation suggests that there may be trade-offs with other traits, or other types of constraints, which limit such evolution.

In theory, traits closely related to fitness are expected to have low heritability, and morphological traits to have higher heritability (Mousseau and Roff 1987). Body size in females is strongly related to reproduction (Honěk 1993), thus even though the measurement is morphological, the trait is linked to fitness. As such, even in the range core, where the tested population is from, it is reasonable to expect some positive selection for larger body size which would reduce genetic variation in the trait. However, we found significant additive genetic variation in female body size. We propose several potential explanations: there may be no ongoing selection on body size to reduce genetic variation, there may be trade-offs with other traits under selection that could help maintain genetic variation, or selection may be variable over time, as seen in other systems (Hunt et al. 2007). In any case, this genetic variation provides the raw material necessary for evolution of body size at the range edge.

In contrast to females, we found no significant additive genetic variation in body mass or thorax width of male beetles in our study here, and correspondingly, there was no clear change in male body mass between the range core and expanding edge (Clark et al., 2022). A reasonable hypothesis is that lack of genetic variation may constrain the evolution of body size in males. Furthermore, despite evolution of increased dispersal during subsequent range expansion (Clark et al. 2022), it could be that there is neither correlated nor direct selection for increased body size in males. Indeed, many insect species are sexually dimorphic in size, with females typically being larger (though no dimorphism and males being larger also occur). Females are larger than males in our study species, which suggests that in general there may not be selection for large size in males even in the context of range expansion. Indeed, in this system, males disperse first, find suitable hosts and emit an aggregation pheromone. This attracts females, who then arrive to mate and reproduce (Cosse et al. 2006). Early dispersal of males may select for early male emergence (protandry), which could in turn favor small size over larger size in males (LoPresti and Morse 2017). However, evidence from other systems suggests that sexual size dimorphism can

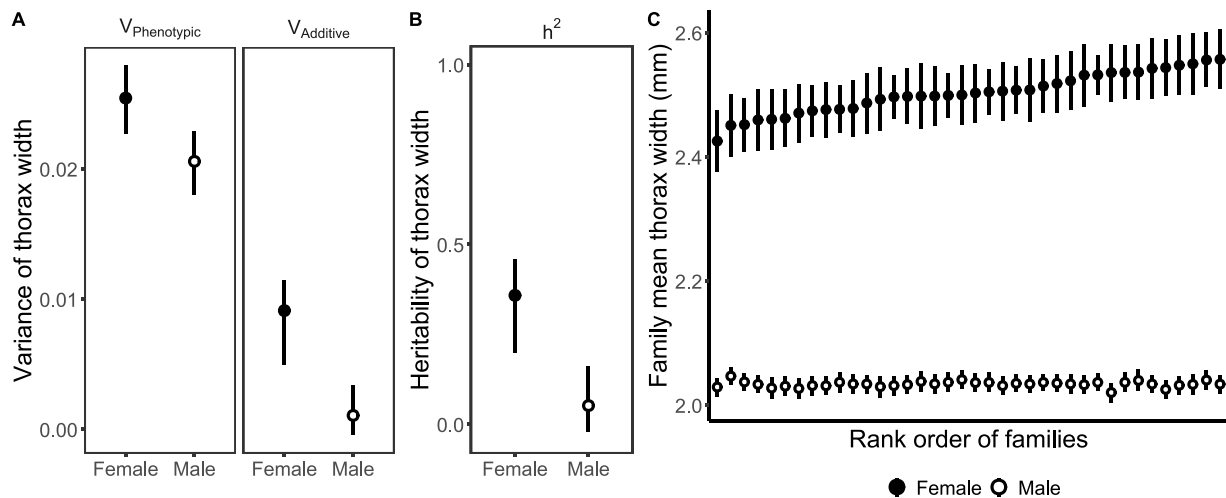


Fig. 2. A. Total phenotypic and additive genetic variation. B. Heritability of thorax width of males and females (means and SDs). C. Mean thorax width for males and females by half-sib family, estimated from the random effects models, ordered on the x-axis by half-sib family mean of thorax width for females.

drive protandry rather than protandry being selected for directly (reviewed in Teder et al. 2021).

The lack of significant heritable variation in males is interesting. Unlike in females where body size is strongly and fairly consistently related to fecundity in many species (Honěk, 1993), the effects of body size in males seems more variable across taxa. In some taxa, large male size is clearly favored by sexual selection, for example in stalk-eyed flies that exhibit male-male competition (Panhuis and Wilkinson 1999) and in tephritids that display to females (Benelli et al. 2015). In other taxa, such as soldier flies, male reproductive success depends upon relative size of males and females, with mismatches (small males with large females, or large males with small females) leading to higher male reproductive success (Jones and Tomberlin, 2021). Clear selection for smaller size is less well documented, but it is thought that there may be costs to large size (Blanckenhorn 2000). These costs can be masked by phenotypic variation in size that arises with differences in availability or quality of resources at the immature stage (Blanckenhorn 2000). It may be that *Diorhabda carinulata* experiences selection for small male size mediated by such proposed costs, and such selection could reduce genetic variation in body size.

To place our finding of low male heritability in size traits into broader context, we searched Web of Science using the search string “heritability AND (“body size” or mass or “thorax width”) AND (insect)” in October 2024. We found 203 papers total, 12 of which reported heritability in body size of both females and males, providing a total of 22 paired measurements from 15 different insect species (Table S1). The heritability of females and males is slightly correlated in these studies, with a confidence interval around the correlation coefficient that slightly overlaps zero (Figure S1, Pearson’s r : 0.39, 95 % CI: −0.04, 0.69). Thorax width in our study, and two measurements from other studies (Piironen et al. 2011 working on *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) and Foelker and Hofstetter 2014 working on *Dendroctonus frontalis* (Coleoptera: Curculionidae)) had a similar pattern of near zero heritability in males, with more substantial heritability in females, and the opposite pattern (near zero heritability in females) was also observed once (Table S1, Figure S1). Thus, there exist other cases where low heritability may constrain the evolution of one sex but not the other. This is a possibility that would be interesting to explore further, particularly in the context of body size dimorphism, and whether heritability or available additive genetic variation might help explain patterns of body size dimorphism in nature.

Overall, our finding of no significant heritability (or evolvability) in male size suggests that lack of genetic variation in males may have hindered evolution of body size during range expansion.

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CRediT author statement

Eliza Clark: Conceptualization, Investigation, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Dan Bean:** Funding acquisition, Conceptualization, Investigation, Writing – review & editing. **Ellyn Bitume:** Conceptualization, Writing – review & editing, Funding acquisition. **Amanda Stahlke:** Investigation, Writing – review & editing. **Paul Hohenlohe:** Conceptualization, Writing – review & editing, Funding acquisition. **Ruth Hufbauer:** Conceptualization, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ruth Hufbauer reports financial support was provided by US Department of Agriculture. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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Data availability

Some data are provided in supplementary files uploaded with the

manuscript, other data are uploaded to external repositories, and working links to these data are provided in the manuscript

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