

SYNTHESIS

Rapid evolution of life-history traits in response to warming, predation and competition: A meta-analysis

Tess Nahanni Grainger^{1,2}  | Jonathan M. Levine² ¹Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada²Princeton University, Princeton, New Jersey, USA**Correspondence**

Tess Nahanni Grainger, Department of Zoology, University of British Columbia, 2212 Main Mall, Vancouver, BC V6T 1Z4, Canada.

Email: tessgrainger@gmail.com

Funding information

Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: Postdoctoral Fellowship; Banting Research Foundation, Grant/Award Number: Banting Postdoctoral Fellowship

Editor: Stephan Munch

Abstract

Although studies quantifying evolutionary change in response to the selective pressures that organisms face in the wild have demonstrated that organisms *can* evolve rapidly, we lack a systematic assessment of the frequency, magnitude and direction of rapid evolutionary change across taxa. To address this gap, we conducted a meta-analysis of 58 studies that document the effects of warming, predation or competition on the evolution of body size, development rate or fecundity in natural or experimental animal populations. We tested whether there was a consistent effect of any selective agent on any trait, whether the direction of these effects align with theoretical predictions, and whether the three agents select in opposing directions on any trait. Overall, we found weak effects of all three selective agents on trait evolution: none of our nine traits by selective agent combinations had an overall effect that differed from zero, only 31% of studies had a significant within-study effect, and attributes of the included studies generally did not account for between-study variation in results. One notable exception was that predation targeting adults consistently resulted in the evolution of smaller prey body size. We discuss potential causes of these generally weak responses and consider how our results inform the ongoing development of eco-evolutionary research.

KEYWORDS

adaptation, biotic interactions, body size, development rate, fecundity, global change, life history, rapid evolution, temperature, traits

INTRODUCTION

The emergence of studies documenting adaptation in real time has led to a growing recognition that evolutionary change can occur simultaneous to ecological change (Endler, 1986; Hendry & Kinnison, 1999; Reznick & Ghilambor, 2005). This convergence of timescales is transforming and uniting the study of ecology and evolution and highlighting the possibility of eco-evolutionary feedbacks in which ecological change drives evolutionary change, which then feeds back to shape ecological dynamics. As a consequence, researchers are increasingly motivated to measure evolutionary change in ecological experiments, and to test how rapid evolution affects

ecological outcomes (Fussmann et al., 2007; Reznick, Losos, et al., 2019). This paradigm shift has been triggered in part by a series of compelling examples of rapid adaptation in response to predation (Endler, 1980; Reznick et al., 1997), competition (Grant & Grant, 2006; Mueller & Ayala, 1981) and climate (Anderson, 1973; Franks et al., 2007) that have helped propel the study of ecology and evolution into a new era. However, while these case studies have convinced us that organisms *can* evolve rapidly, this still leaves the open question of how often they do.

Fortunately, this growing interest in experimental evolution has resulted in a substantial number of studies in animal populations that have tested for rapid evolution in response to three major agents of selection:

temperature, predation and competition. While this research has been conducted in a variety of animal study systems, a common thread that links many of these studies is a focus on the evolution of life-history traits, as these traits translate individual fitness into population dynamics and thus provide a direct link between ecology

and evolution (Roff, 2002; Stearns, 1989). The growing body of empirical research testing for genetically based changes in traits such as body size, development rate and fecundity in response to common agents of selection provides an exciting opportunity to quantitatively test for generalities in rapid evolutionary responses. Moreover,

TABLE 1 Theoretical predictions and explanations for how warming, predation and competition affect the evolution of body size, development rate and fecundity

Agent of selection	Life-history trait	Predicted evolved response	Explanations from theory
Warming	Body size ^a	Smaller	<ul style="list-style-type: none"> As warming increases metabolic demands, large individuals with high metabolic needs suffer increased mortality or reduced fecundity (Partridge & French, 1996)^b(Atkinson, 1994)^b Warming weakens the positive relationship between body size and fecundity, which relaxes selection for large body size (Arendt, 2015) Organisms adapted to cold have higher growth efficiency, so larger individuals are produced per unit of resource at low temperatures (Partridge & French, 1996)^b A combination of thermal constraints on juvenile mortality, maximal body size and population growth rates contributes to the evolution of smaller body size at warmer temperatures (Angilletta, 2009)^b
	Development rate	Slower	<ul style="list-style-type: none"> Slower development rates evolve to counteract a plastic acceleration of development at high temperatures (Atkinson (1994); Clarke (2003)^b)
	Fecundity	Higher or lower	<ul style="list-style-type: none"> At high temperatures, faster somatic growth rate allows individuals to escape juvenile mortality, reducing the benefit of producing large offspring and making it beneficial to produce more smaller offspring (Yampolsky & Scheiner, 1996)
Predation	Body size	Smaller or larger	<ul style="list-style-type: none"> When predation targets adults or targets all life stages equally, smaller adult body size allows individuals to reach maturity and reproduce before being eaten (Gadgil and Bossert (1970); Taylor and Gabriel (1992); Abrams and Rowe (1996)) When predation is gape-limited or targets juveniles, larger adult body size allows individuals to escape predation (Gadgil and Bossert (1970); Stearns (1983)^b; Urban (2007))
	Development rate	Faster or slower	<ul style="list-style-type: none"> When predation targets adults or targets all life stages equally, faster development allows individuals to reproduce before being eaten (Taylor and Gabriel (1992); Abrams and Rowe (1996); Urban (2007)) When predation is gape-limited or targets juveniles, slower development allows individuals to invest more into growth and reach a size refuge from predation (Day et al., 2002; Taylor & Gabriel, 1992)
	Fecundity	Higher or lower	<ul style="list-style-type: none"> Increased mortality under predation and the resulting increase in available resources favours a faster pace of life that includes the production of many offspring (Gadgil & Bossert, 1970), particularly when predation is gape-limited or targets juveniles (Stearns (1983)^b) Predation that targets adults or targets all life stages equally favours lower investment into reproduction (Stearns (1983)^b)
Competition	Body size	Larger or smaller	<ul style="list-style-type: none"> In competitive conditions, larger body size provides a competitive advantage (Wright et al., 2019)^b Competitive conditions where resources are limited favour small individuals with lower resource requirements (Boyce, 1984)^b
	Development rate	Slower	<ul style="list-style-type: none"> Low resource availability resulting from competition favours individuals with slower development rate (Gadgil & Bossert, 1970) or a generally slower pace of life (Wright et al., 2019)^b
	Fecundity	Lower	<ul style="list-style-type: none"> Low resource availability resulting from competition favours individuals with lower investment into reproduction (Gadgil and Bossert (1970); Schaffer and Gadgil (1975)), smaller clutches of larger individuals (Parker & Begon, 1986) or a generally slower pace of life (Wright et al., 2019)^b

Note: Body size is size at sexual maturity, development rate is time to sexual maturity, and fecundity is lifetime fecundity. Warming is an increase in temperature that remains below a species' critical threshold and competition is intraspecific competition. Explanations from theory come from mathematical models unless otherwise noted.

^aNote that the widely cited and empirically investigated 'body size-temperature rule' of smaller body size at higher temperatures (Atkinson, 1996) and 'Bergmann's rule' of a positive relationship between latitude and body size (Bergmann, 1848) are not included here, as the former describes plastic effects of warming on body size (Atkinson, 1994; Kingsolver & Huey, 2008), while the latter has unclear links to both temperature and evolutionary change (Partridge & Coyne, 1997; Watt et al., 2010).

^bPrediction comes from verbal reasoning or a synthesis, not a mathematical model.

these traits transcend animal taxa, facilitating generalisation across systems in this emerging area of research.

Generalisation may be possible given that evolutionary theory makes some clear predictions for how temperature, predation and competition select on body size, development rate and fecundity (Table 1) (Abrams & Rowe, 1996; Arendt, 2015; Gadgil & Bossert, 1970; Urban, 2007). For example, predation that targets adults or that targets all life stages equally is thought to favour the evolution of smaller body size, faster development rate and higher investment in fecundity (Abrams & Rowe, 1996; Taylor & Gabriel, 1992). By contrast, predation that is gape-limited or targets juveniles should select in the opposite direction (Table 1) (Day et al., 2002; Gadgil & Bossert, 1970; Urban, 2007). Increasing temperature, meanwhile, is generally predicted to favour the evolution of smaller body size and slower development rates, although the mechanisms that underly these responses and the links between plastic and evolutionary responses to temperature have yet to be fully resolved (Table 1) (Atkinson, 1994; Partridge & French, 1996; Yampolsky & Scheiner, 1996). Finally, theory focused on interspecific competition is more ambiguous. For example much of the focus of competition on trait evolution centres around character displacement with unclear links to general life-history traits (Schluter & McPhail, 1992), while classic life-history theory and more recent extensions predict that intensified competition could either cause the evolution of smaller body size or traits associated with a slower pace of life such as larger body size, slower development and lower fecundity (Boyce, 1984; Gadgil & Bossert, 1970; Wright et al., 2019) (Table 1).

If life-history traits do indeed evolve consistently across taxa in response to a single agent of selection, we can then ask if multiple agents select in opposing or parallel directions. Answering this question is important because organisms live in complex environments and are rarely, if ever, subjected to a single selective pressure. Moreover, as temperatures rise and species invade new areas under global change, determining whether warming selects in the same or the opposite direction as biotic agents of selection is becoming increasingly critical for forecasting adaptation to climate change (Alexander et al., 2016; De Meester et al., 2019; Tseng & O'Connor, 2015). For example if warming and competition both select for smaller body size, as predicted (Table 1), existing or novel competitive interactions could hasten species' adaptation to a warming climate (Osmond & de Mazancourt, 2013). Conversely, if predation selects for a larger body size, as is predicted for certain predators (Table 1), predation pressure could hinder species' ability to adapt to a warming climate. Unfortunately, we currently do not know whether life-history evolution in response to temperature occurs in the same or the opposite direction as life-history evolution in response to predation or competition.

To address these knowledge gaps, we conducted a meta-analysis of 58 studies that document the effects of warming, predation or competition on the evolution of body size, development rate or fecundity in either natural or experimental animal populations. Importantly, all of the studies we included used common gardens to separate genetic from plastic effects. Previous reviews have contributed qualitative assessments of the evidence for rapid evolutionary change in general (Kawecki et al., 2012; Reznick & Ghalambor, 2005; Thompson, 1998) or in response to global change (Gienapp et al., 2008; Jump & Penuelas, 2005; Sheridan & Bickford, 2011), while quantitative reviews have assessed the strength and direction of phenotypic selection (Kingsolver et al., 2001; Siepielski et al., 2019) and the speed of evolutionary change (Hendry & Kinnison, 1999) in natural populations. Despite the important contributions of these prior efforts, none provide a quantitative and systematic assessment of the frequency and direction of rapid evolutionary trait change in response to shared ecological agents of selection.

We addressed three questions with our meta-analysis: (1) Is there a consistent effect of either warming, predation or competition on body size, development rate or fecundity, and do any of these effects align with theoretical predictions? (2) Do our three focal agents of selection act in opposing directions on any life-history trait? (3) Which features of the study systems predict the strength and direction of life-history evolution in response to warming, predation and competition? While we recognise that in nature, traits are complex, multivariate and constrained by genetic correlations, and that agents of selection are numerous and interacting, we chose these three traits and these three agents of selection because they are commonly manipulated or measured in empirical studies, theory generates predictions for these relationships, they are relevant to ecological dynamics, and they can inform our understanding of how populations respond to global change.

MATERIALS AND METHODS

Data collection

In August 2020, we searched the Web of Science for papers that included (“evolution” OR “adaptation”) AND (“temperature” OR “warming” OR “thermal” OR “predators” OR “predation” or “competition” or “competitors”) in the title. This returned 595 results, all of which were assessed for inclusion (detailed search methods in Supporting Information). We then searched 20 previous reviews and meta-analyses on related topics for additional studies that met our inclusion criteria (see list in Supporting Information). Finally, we searched all of the studies that met our inclusion criteria for further studies to include.

We used the following criteria to determine inclusion in our meta-analysis. Studies had to: (1) quantify evolutionary change in response to one or more of our three focal selective agents (temperature, predation, competition) (2) compare at least one group that we could use as a control group (e.g. lower temperature, no predation, no competition) to at least one group that we could use as a treatment group (e.g. higher temperature, predator present, competitor present) (3) measure at least one of our three focal life-history traits (body size, development rate, fecundity) in both the control and treatment group and (4) separate evolutionary change from maternal effects and plasticity by growing individuals under common conditions for at least one generation (i.e. a common garden).

We included both ‘experimental’ studies in which the selective agent was imposed by the researcher either in the laboratory or in the field (e.g. experimentally imposed presence or absence of a predator) and ‘natural’ studies in which the selective agent varied naturally across space or time (e.g. comparison of streams with predators to streams without). We excluded studies that focused on evidence from the fossil record, but placed no other restrictions on study duration and instead included the number of generations of selection in our models to determine whether this affected the outcome of evolution (see Data Analysis). While the definition of ‘rapid evolution’ has been debated (Hairston et al. 2005; Thompson, 1998), this term was widely employed by the authors of the included studies to describe evolutionary change that occurs on the same timescale as ecological change and experimental investigations, and so we use that term here as well. We restricted competition studies to those that focused on resource competition (i.e. no mate competition). We also excluded studies for which it was not clear that the selective agent of interest was the principal factor driving trait change (e.g. studies that assessed trait change across latitudinal or urbanisation gradients as a proxy for temperature change). Our inclusion criteria resulted in the exclusion of rapid evolution studies that focused on the effects of other environmental variables (e.g., drought, CO₂), other biotic interactions (e.g. disease, mutualisms) or other anthropogenic changes (e.g. fish harvesting, habitat fragmentation). Our criteria also excluded studies that used population growth rate rather than life-history traits as the response, that did not separate plastic from heritable responses, that used selective mortality or selection gradients as the response, or that imposed artificial selection. Details of our study selection criteria are provided in the Supporting Information.

Our selection criteria resulted in a dataset that included 58 studies focused on animals and three studies focused on plants. We deemed the three plant studies to be too few to make meaningful comparisons and therefore restricted our analysis to animal studies. The 58 remaining studies encompassed 33 focal species (14 aquatic and 19 terrestrial) spanning 15 orders (Figure S1). All

but two of the included studies were conducted with ectothermic organisms (the exceptions were studies with rabbits (Williams & Moore, 1989) and mice (Barnett & Dickson, 1984)). Many of the 58 studies measured multiple life-history traits, included multiple focal species, or assessed the effect of multiple selective agents, and thus our final dataset included 124 unique effect sizes (data points).

For each unique effect, we extracted the mean trait value and the sample size of both the control group and the treatment group. We extracted these data directly from tables, from figures using WebPlotDigitizer (version 4.4) (Rohatgi, 2020), or from raw data obtained from supporting information, from online repositories or by contacting the authors. We used methods described in Hozo et al. (2005) to calculate means from box plots. We used trait values measured on individuals after they had been grown for at least one generation under common garden conditions. Some studies included more levels than just a control and treatment group or measured the same life-history trait using multiple metrics or under multiple common garden conditions. In these cases, we used a priori rules detailed in the Supporting Information to select data in a consistent manner.

For each study, we recorded the taxonomic order of the focal species, whether the variation in the selective environment was ‘natural’ or ‘experimental’ (described above), and the number of generations that elapsed while selection was imposed (details in Supporting Information). For predation studies, we also recorded the life stage (adult or juvenile) targeted by the focal predator, and for warming studies, we recorded the temperature difference between the control and treatment.

Data analysis

We quantified the effect of the selective agents on the evolution of life-history traits as the ln-transformed response ratio (LRR), which was calculated as:

$$LRR = \ln(X_T/X_C)$$

where X_T is the mean trait value of the replicate populations (or individuals, clones or families; see note below) in the treatment group, and X_C is the mean trait value of the replicate populations (or individuals, clones or families) in the control group. Response ratios quantify the proportional change between the control group and the treatment group. Log response ratios are used because n -fold increases and n -fold decreases are of the same magnitude (but of opposing sign) and because the ln transformation creates a more linear and normally distributed response amenable to statistical tests. A log response ratio of zero indicates no treatment effect, while a positive log response ratio indicates a positive effect and a negative log response ratio indicates a negative effect. Funnel plots confirmed

TABLE 2 Results of targeted models used to identify significant modifiers

Trait	Selective agent	Fixed factors in model	Significance	Figure	Percentage of effect sizes significantly different from zero
Warming	Body size	Study type	NS	NA	3/11 (27%)
		Generations	NS	NA	
		Temp difference	NS	NA	
	Development rate	Study type	NS	NA	3/12 (25%)
		Generations	NS	NA	
		Temp difference	NS	NA	
	Fecundity	Study type	NS	NA	2/6 (33%)
		Generations	NS	NA	
		Temp difference	NS	NA	
Predation	Body size	Generations	NS	NA	6/16 (37%)
		Study type	NS	NA	
		Predated life stage	$p = 0.002$	Figure 2	
	Development rate	Generations	NS	NA	3/8 (37%)
		Predated life stage	NS		
	Competition	Fecundity	Generations	NS	NA
Body size		Generations	$p = 0.001$	Figure S6	3/8 (37%)
		Development rate	Generations	NS	NA
	Fecundity	Generations	NS	NA	1/7 (14%)

Significant results are bolded and have an associated figure. NS indicates that $p > 0.1$. 'Percentage of effect sizes significantly different from zero' indicates (for each of the nine selective agent by trait combinations) the percentage of effect sizes in our dataset that had 95% CIs that did not cross zero (shown in Figures S3–S5). Only studies that had replication at the population level (and thus population-level error associated with them) were included in the calculation of this percentage.

that the data showed lower variance at a higher sample size and were symmetric around the mean (Palmer, 1999), suggesting no evidence of publication bias (Figure S2).

We used a series of three model types to address our three research questions. First, to determine whether there was a consistent effect of any selective agent on any life-history trait (Question 1), we ran a global linear mixed effects model. We used this model to calculate the overall mean effect size and associated confidence interval for each of our nine trait by selective agent combinations in order to determine whether any of these mean effects were significantly different from zero. This global model had log response ratio as the response variable, life-history trait and selective agent as fixed effects, study and taxonomic order as random effects, and was weighted by the square root of the pooled sample size. We used the package 'emmeans' to estimate the mean effect size for each of our nine traits by selective agent combinations and the 95% confidence intervals surrounding these means. 95% bootstrapped confidence intervals produced slightly wider confidence intervals and qualitatively the same results. When confidence intervals for a type of effect do not overlap zero, that effect is considered significant.

Second, to determine whether our three focal selective agents acted in opposing directions on a given trait (Question 2), we used three separate, trait-specific, linear mixed effects models (one each for body size, development

rate and fecundity). These models had log response ratio as the response variable, selective agent as the fixed effect, study and taxonomic order as random effects, and were weighted by the square root of the pooled sample size. We used ANOVA to test whether 'selective agent' had a significant effect on evolutionary trait change for a given trait. For any significant effect of selective agent, we then performed pairwise post hoc comparisons (all possible pairwise *t*-tests) to determine which pairs of selective agents differed in their effects, and for these, we examined whether the responses were of opposite sign (which would indicate an opposing effect of two selective agents). These additional models were required to answer Question 2 because in our global model, neither an overall effect of selective agent nor a significant trait by selective agent interaction would reveal whether the selective agents acted in opposing directions on a given trait.

Finally, to determine which attributes of the study system (i.e. modifiers) influenced the effect of the selective agents on trait evolution (Question 3), we ran nine separate linear mixed effects models (all trait by selective agent combinations), each on the relevant subset of the full dataset. We conducted nine separate analyses rather than including modifiers in the global model because certain modifiers were only relevant to certain selective agents or traits (e.g. temperature span between treatments only pertains to warming studies) and because

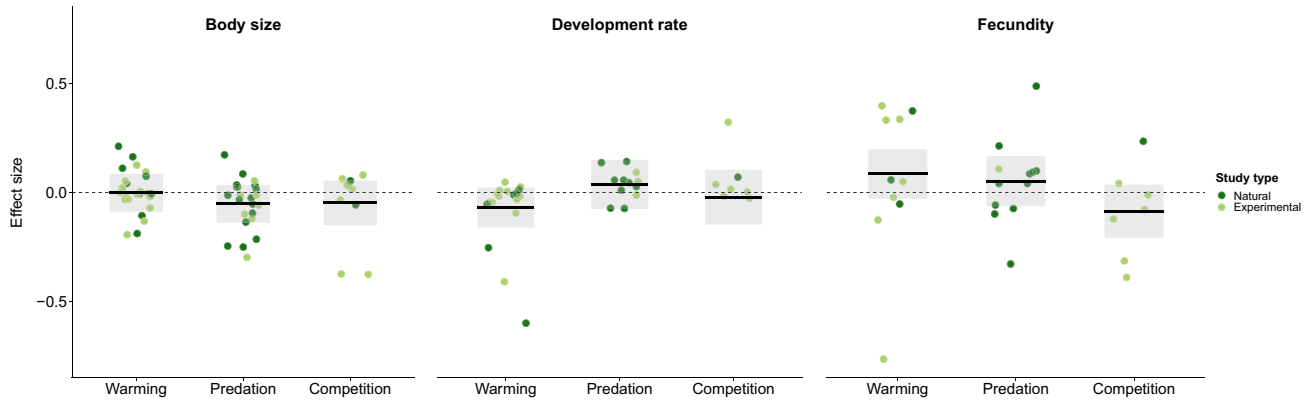


FIGURE 1 Effect of warming, predation and competition on evolutionary change in body size, development rate and fecundity. A positive effect size indicates that the selective agent (warming, predation or competition) was associated with the evolution of larger body size, faster development rate or higher fecundity, while a negative effect size indicates the opposite. Data points show raw effect sizes and means and 95% confidence bands are from mixed effects models. All confidence bands overlap zero, indicating a lack of significant effect across studies of any selective agent on any life-history trait. Dark green points indicate studies in which the agent of selection (warming, predation or competition) varied naturally across space or time, and light green points indicate studies in which the agent of selection was experimentally imposed.

some modifiers could only be tested on some trait-selective agent combinations due to limited data. Each model had log response ratio as the response variable, number of generations and study type (experimental or natural) as fixed effects, study and taxonomic order as random effects, and was weighted by the square root of the pooled sample size. The three temperature models also included the degree difference between the control and treatment (treatment temperature minus control temperature in °C) as a fixed effect, and the three predation models included the life stage targeted by the predator (juvenile or adult) as a fixed effect. To minimise the effects of small sample size, we only analysed contrasts with three or more data points in each group (Borenstein et al., 2009). In these models we first tested for all possible interactions and then dropped all nonsignificant interactions and re-tested and reported the significance of fixed effects in simplified models.

In all of the above models, we accounted for the lack of independence among effects from the same study, the lack of taxonomic independence for different focal species, and the differences in reliability of results from studies with different sample sizes as follows. Given that many studies in our dataset measured multiple traits and therefore contributed more than one effect size, we included study identity as a random effect. Similarly, to account for the taxonomic non-independence of study species, we included the order of the focal species as a random effect in our models. We used order because this taxonomic rank has been shown to be suitable for classifying phenotypic divergence as it provides a homogenous unit of comparison (i.e. it aligns closely with absolute dates of evolutionary origin) (Bennett et al., 2021; Holt & Jønsson, 2014), and is not so broad as to miss meaningful phenotypic differences. Removing order as a random effect did not affect any of our results.

In order to downweight effect sizes calculated with low population-level replication, given the assumption that effect sizes from studies with large sample sizes will be more precise than effect sizes from studies with small sample sizes, we weighted all of our analyses by the square root of the sample size pooled across the control and treatment groups (Hargreaves et al., 2020; Kambach et al., 2020). We used this method rather than weighting effect sizes by the pooled variance (as common in meta-analyses) because 34% of our studies lacked variance estimates at the level of the population (with ‘population’ defined as a group of potentially interbreeding individuals), which was the unit of interest for our analyses (Hargreaves et al., 2020; Hoeksema et al., 2010). Although population-level replication is the gold standard for experimental evolution, a lack of population-level replication is a widespread issue in the field (Hendry, 2019). Of the 58 studies included in our analysis, 38 studies had replication at the population level (i.e. two or more replicate control populations and two or more replicate treatment populations), while the remaining 20 studies had replication at the individual, clone or family level. We considered populations to be replicates if they were geographically or genetically distinct or if the authors stated that they were unique. Our weighting method allowed us to include studies that lacked population-level replication, which was important for maximising our sample size and avoiding potential biases that could emerge if population-level replication was associated with other study attributes (Englund et al., 1999; Kambach et al., 2020).

To determine what percentage of studies in each of our nine categories had an effect size that was significantly different from zero (confidence intervals not overlapping zero), we calculated 95% confidence intervals on the log response ratio for each study using the metafor package in R. We could only do this for studies

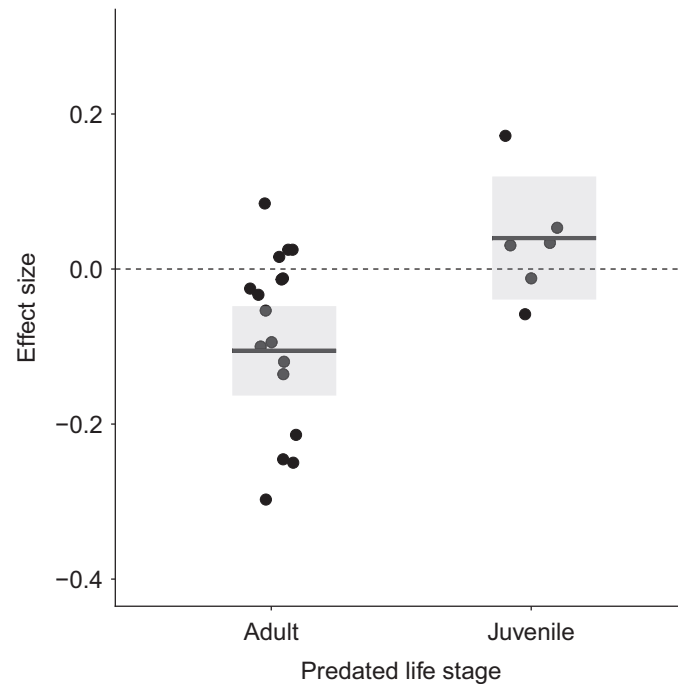


FIGURE 2 Effect of predated life stage on body size evolution. A positive effect size indicates that predation was associated with the evolution of larger body size at maturity, while a negative effect size indicates that predation was associated with the evolution of smaller body size at maturity. Data points show raw effect sizes and means and 95% confidence bands are from mixed effects models.

that had replication at the population level because only these studies had population-level error for the control and treatment groups. These percentages are reported in Table 2, and means and 95% CIs for all effect sizes with population-level replication are shown in forest plots (Figures S3–S5).

All analyses were conducted in R (version 4.0.4), all models were constructed using the package ‘lme4’, and all figures were made using the ‘ggplot2’ package. For all analyses, we tested the significance of fixed effects using a likelihood ratio test (‘drop1’ function with a ‘Chisq’ distribution). All data supporting this research are available on the Dryad Digital Repository (Grainger & Levine, 2021).

RESULTS

Question 1. Is there a consistent effect of any selective agent on any life-history trait?

We found no evidence for consistent effects of warming, predation or competition on the evolution of body size, developmental rate or fecundity, as the 95% confidence intervals around the mean effect size overlapped zero for all nine trait by selective agent combinations (Figure 1). This absence of consistent rapid evolutionary responses to warming, predation and competition could result from weak effects within studies, or alternatively, from strong effects within studies but the large variance and/

or opposing sign across studies. The first alternative of weak effects within studies was supported by our finding that of the 81 effect sizes from studies with population-level error in our dataset, only 31% were significantly different from zero (Table 2, Figures S3–S5).

Question 2. Do selective agents tend to select in opposing directions on a given trait?

Despite no overall effect of any of our focal selective agents on trait evolution (Figure 1), there was a significant effect of selective agent on development rate ($\chi^2 = 6.09, p = 0.048$) that post hoc pairwise tests revealed arose because predation and warming differed marginally in their selective effects on this trait ($t = -2.24, p = 0.067$): predation modestly accelerated development and warming modestly slowed development. There was no effect of selective agent on the evolution of body size ($\chi^2 = 2.40, p = 0.30$) or fecundity ($\chi^2 = 3.19, p = 0.20$).

Question 3. Which attributes of the study system predict evolution in response to the selective agents?

Across the nine selective agent by trait combinations, the type of selection imposed (natural or experimental) never significantly affected trait evolution (Table 2). Likewise, the temperature range examined in warming studies did

not affect trait evolution (Table 2). The number of generations in the study did not generally affect trait evolution, except in the case of body size evolution in response to competition. Here, effect sizes were more negative (indicating the evolution of smaller body sizes) when studies allowed more generations of selection to elapse ($\chi^2 = 10.59$, $p = 0.001$, Table 2, Figure S6). However, we interpret this result with caution, as it was driven by two studies with a high number of generations and strongly negative effect sizes, and these came from the same focal study system and investigator (Terhorst, 2010, 2011).

Our moderator variable analysis also revealed that the effect of predation on body size evolution depended on the life stage targeted by the predators ($\chi^2 = 8.99$, $p = 0.002$, Table 2). Specifically, predation on adults led to the evolution of smaller prey body size, while predation on juveniles had no consistent effect on the evolution of body size (Figure 2).

DISCUSSION

Given the growing acceptance that evolutionary change can occur simultaneous to ecological change and the many outstanding empirical studies that have contributed to this paradigm shift, ecologists and evolutionary biologists may now expect that rapid evolution will occur frequently, and that when it does, that we will be able to detect it. We searched for evidence of consistent evolutionary change in some of the most commonly measured traits in response to some of the most commonly manipulated selective agents, and for the most part, did not find it. We found weak overall effects of warming, predation and competition on the evolution of key life-history traits, as none of the nine selective agent by life-history trait combinations that we examined had an overall effect that was significantly different from zero (Figure 1), and only 31% of studies' individual effects sizes differed from zero (Table 2, Figures S3–S5). Moreover, few attributes of the included studies accounted for between-study variation in results (Table 2). Apart from the notable exception that predation targeted at adults consistently resulted in the evolution of smaller body size (Figure 2), the major result of our analysis is the lack of strong or consistent effects of key ecological factors on the rapid evolution of life-history traits. Given this, we focus our discussion on how surprising this result should be in light of existing theory and previous data syntheses, and what our findings can contribute to our understanding of evolution on ecological time scales.

Should we expect rapid evolution of life-history traits?

We based our expectations for how warming, predation and competition would affect the evolution of life-history

traits on theory wherever it was available (Table 1), and in only one case did our results support theoretical expectations: predation targeting adults selected for smaller body size (Figure 2). Interestingly, of the three selective agents included in our analysis, predation has the most well-developed theory with the clearest links to mechanisms captured in empirical research (Table 1). Several iterations of this theory predict that when predation targets adults, individuals that mature earlier and at a smaller size are more likely to reproduce before being eaten (Abrams & Rowe, 1996; Gadgil & Bossert, 1970; Taylor & Gabriel, 1992).

In contrast, the theoretical links between warming and body size have largely focused on extrapolating from the widely documented plastic reduction in body size at warm temperatures and the observed positive association between latitude and body size, both of which have unclear links to adaptive trait change (Kingsolver & Huey, 2008; Watt et al., 2010). On the empirical side, an interest in the potential for adaptive responses to ongoing global change has prompted meta-analyses and reviews focused on warming as a selective agent. Interestingly, these studies also report no or weak effects of temperature on trait evolution. For example a meta-analysis that focused on selection gradients in plants, birds and mammals found no evidence of stronger selection for small body size at warmer temperatures (Siepielski et al., 2019), and a meta-analysis on birds that combined plastic and evolved responses found no evidence that recent global warming has systematically affected morphological traits (Radchuk et al., 2019). Likewise, three other reviews report a lack of evidence for microevolution driving changes in body size with warming (Gardner et al., 2011; Gienapp et al., 2008; Teplitsky & Millien, 2014).

While the effect of predation on trait evolution has clear theoretical predictions and the effect of warming on traits benefits from a large body of empirical work, the effect of competition on the evolution of life-history traits has neither. Theoretical expectations for the effects of competition on life-history evolution remain unclear, and stem primarily from classic life-history theory focused on *r* vs. *K* selection (Gadgil & Bossert, 1970; Pianka, 1970; Wright et al., 2019). However, this theory focuses on intraspecific density effects, while most studies investigating the effect of competition on the evolution of life-history traits (12 of the 14 included studies) manipulate interspecific competition. Additionally, theory on interspecific competition tends to emphasize trait change relative to competitor traits (Dayan & Simberloff, 2005; Schluter & McPhail, 1992), which suggests that perhaps evolved trait change in response to competition will be competitor-specific and that general effects of competition on life-history trait evolution may be unlikely.

Overall, a lack of clear theoretical expectations or previous empirical support for general trends in how warming and competition select on life-history traits

make our finding of weak effects for these two agents somewhat less surprising. Additionally, even in cases where strong and directional selection is imposed, low heritability or low genetic variation can constrain trait evolution (Chevin et al., 2010), which may also have contributed to the generally weak responses reported here.

Should we expect to detect rapid evolution of life-history traits when it occurs?

An alternative explanation for the weak evidence of rapid evolutionary change reported here is that investigators were simply unable to detect the evolutionary change occurring in their studies. This seems likely in at least some cases, given the difficulties inherent in deciding which traits to measure and how to do so. For example the decisions that go into quantifying even the simplest trait measurements (e.g. body weight vs. length, reproduction at first clutch vs. lifetime reproduction) mean that adaptive responses in unmeasured dimensions will be missed (Germain et al., 2018; Grainger et al., 2021). Indeed, while our analysis includes the three life-history traits most commonly measured in empirical studies, additional data on the evolution of other key life-history traits such as longevity would give a more complete answer to our research questions.

In addition, recent evidence suggests that trait evolution may be missed if sampling intervals are not on an appropriate (yet often unknown) time scale (Rudman et al., 2021). Knowing how many generations are required for trait evolution is difficult, and decisions around experimental duration are usually constrained by logistical considerations. Indeed, while our tentative finding of a stronger effect of competition on body size when more generations elapsed during selection should be interpreted with caution, it supports the idea that experiments that allow more generations to elapse may be more likely to capture trait evolution (Figure S6, Table 2).

Finally, while common gardens are essential for separating evolved trait change from plastic responses, they are also subjectively chosen and may mask evolved change that would be detectable under other conditions (Hendry, 2019; Irschick, 2003). Indeed, a majority of the studies included here (39/58) measured traits under multiple common garden conditions that varied in resource type, temperature or predation pressure, and some of these studies reported that an evolved trait change was detected under only some common garden conditions (Van Doorslaer et al., 2007; Tobler et al., 2015; Tseng & O'Connor, 2015).

Due to the issues associated with testing for evolved trait change, integrating across organisational scales to evaluate rapid evolution by incorporating responses

such as genomic data (McGaughan et al., 2021; Rudman et al., 2018) and population growth rates (Collins, 2011; Futuyma, 1970; Germain et al., 2020; Hart et al., 2019; Lawrence et al., 2012) may be the most productive way forward. As the former approach has the benefit of offering insight into the genetic underpinnings of observed phenotypic change and the latter provides a direct link to ecological dynamics, both sources of information will be invaluable in efforts to fully understand the causes and consequences of rapid evolution.

Implications for global change

We found modest evidence for opposing selection by warming and predation on development rate, which manifested as a significant effect of selective agent on this trait ($p = 0.048$) and a marginally significant post hoc test that revealed that warming caused the evolution of a slower development rate than did predation ($p = 0.067$). Although these marginal results should be interpreted with caution, it is worth noting that the direction of these trends match theoretical predictions (Table 1), and may indicate that strong predation pressure could hamper evolutionary responses of development rate to warming. Additionally, although both development rate and fecundity are less commonly measured than body size in rapid evolution experiments, development rate may be a better candidate than fecundity for future work, as it tended to show a stronger response to treatments and less variability across studies (Figure 1).

In the context of climate change, it has been proposed that aquatic organisms may be more likely than terrestrial organisms to experience an evolved reduction in body size at warmer temperatures due to a warming-induced reduction in the availability of dissolved oxygen (Audzijonyte et al., 2019). However, we note that none of the six studies in our dataset that investigated the effect of warming on body size in aquatic organisms found a significant effect (studies indicated by asterisks in Figure S3). Overall, the lack of effect of warming on evolved trait change reported here may indicate that plastic responses (Gienapp et al., 2008) or adaptive changes in other traits such as phenology (Radchuk et al., 2019; Réale et al., 2003) or behaviour (Berthold et al., 1992) may contribute more to species' evolutionary responses to climate change than the evolution of life-history traits.

Areas where more data are needed

While growing interest in questions centred around evolutionary change that occurs on ecological timescales has produced the body of empirical research that enabled this analysis, in some cases a lack of data precluded definitive conclusions about the effects of warming,

predation and competition on life-history evolution. A prime example is the effect of competition, which was the most data-poor of the three selective agents in our study. Of particular need are more studies focused on the effect of competition on life-history evolution that allow a high number of generations (>50) to elapse, which of course will be most feasible for organisms with short generation times (Terhorst, 2010, 2011) (Figure S6). Likewise, only two studies that met our inclusion criteria tested the effect of intraspecific competition on the evolution of life-history traits (Santos et al., 1997; Terhorst et al., 2010), despite the emphasis on intraspecific density dependence in classic life-history theory (Boyce, 1984; Gadgil & Bossert, 1970; Pianka, 1970). In addition, while we treated each of our selective agents as independent in this analysis, interactions and feedbacks between temperature, competition and predation are likely to be common nature; for example both predation and temperature can alter the competitive environment through effects on density (Reznick, Bassar, et al., 2019). Despite this, only five of the 58 studies in our dataset tested the effect of more than one of our three selective agents (Cavalheri et al., 2019; Terhorst, 2010; Terhorst et al., 2010; Tseng et al., 2019; Tseng & O'Connor, 2015). Investigations into the combined effects multiple agents of selection on the evolution of life-history traits should be considered an important area for future investigation.

While our dataset included 33 species spanning 15 orders, many taxonomic groups were over-represented, and for each of our three selective agents, certain study systems were disproportionately studied (Figure S1). Specifically, warming experiments often focused on zooplankton and flies, predation studies most often used zooplankton or fish and competition studies often used flies (Figure S1). It is worth considering the benefits of testing these questions in less commonly used systems based either in the laboratory (e.g. bean beetles, flour beetles, protists) or field (e.g. lizards, frogs). Some of these other organisms also have short generation times and measurable traits and can be reared in common gardens, and have been successfully used in rapid evolution research (Kawecki et al., 2012).

It would also be informative to examine whether the weak evolutionary responses we report here tend to arise from replicate populations consistently showing weak or no response to a given selective agent or to replicate populations showing strong but divergent (non-parallel) responses. Along these lines, while we focused on changes in mean trait values indicative of directional selection by each of our agents, an interesting follow-up question is whether individual-level (within population) variance differed between the control and treatment groups, which would suggest stabilising or disruptive selection. Unfortunately, the studies in our dataset usually reported only population-level means and variances, and so the population and individual level data required to address these questions were not available. However,

the trend towards both population-level replication (Hendry, 2019) and open access data will hopefully make these types of analyses possible in the near future.

Finally, it would also be interesting to compare the magnitude and direction of plastic versus evolved responses to warming, predation and competition, as plastic trait change can have ecological consequences of comparable magnitude to evolved trait change (Yamamichi et al., 2011). Making this comparison requires experiments that measure traits on individuals collected directly from experimental conditions, before common garden rearing. Of the 58 studies in our dataset, only 10 reported pre-common garden trait measurements. Studies that compare plastic and genetic responses would also shed light on how often plasticity and genetically based trait change occur in the same direction ('cogradient variation') or opposite direction ('counter-gradient variation'), and whether these outcomes are associated particular selective agents or life-history traits.

CONCLUSION

Overall, we found little evidence for strong or consistent effects of warming, predation and competition on the evolution of body size, fecundity and development rate, with the notable exception of an effect of predation on body size that aligned with theoretical expectations. Although for some of the nine traits by selective agent combinations examined here, more studies across a broader range of taxa would help confirm our findings, the evidence compiled here suggests that rapid evolution of life-history traits in response to these three major selective agents is either rare, weak or not readily detectable in experiments. Rather than discouraging investigations of rapid life-history evolution, these findings should motivate researchers to think deeply about the conditions under which life-history traits are likely to rapidly evolve, and how best to capture this evolution when it happens.

ACKNOWLEDGEMENTS

We thank W. Petry, A. Hargreaves, M. O'Connor, S. Otto, K. Gotanda, R. Germain and the Germain Lab for valuable discussions about meta-analyses and rapid evolution. We thank the authors of the included studies for their research and for making their data accessible. We thank two anonymous reviewers for their helpful comments and suggestions. Funding was provided by an NSERC Postdoctoral Fellowship and a Banting Postdoctoral Fellowship to TNG and Princeton Start-Up funds to JML.

AUTHORS CONTRIBUTIONS

TNG designed the study, collected the data, conducted the analyses and wrote the manuscript, and JML

contributed substantially to the study design and to revisions.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13934>.

DATA AVAILABILITY STATEMENT

All data supporting our results are published on Dryad at <http://dx.doi.org/10.5061/dryad.xgxd254hh> and are referenced in the Data Analysis section of the manuscript.

ORCID

Tess Nahanni Grainger  <https://orcid.org/0000-0002-6094-0526>

Jonathan M. Levine  <https://orcid.org/0000-0003-2857-7904>

REFERENCES

- Abrams, P.A. & Rowe, L. (1996) The effects of predation on the age and size of maturity of prey. *Evolution*, 50, 1052–1061.
- Alexander, J.M., Diez, J.M., Hart, S.P. & Levine, J.M. (2016) When climate reshuffles competitors: a call for experimental macroecology. *Trends in Ecology & Evolution*, 31, 831–841.
- Anderson, W.W. (1973) Genetic divergence in body size among experimental populations of *Drosophila pseudoobscura* kept at different temperatures. *Evolution*, 27, 278–284.
- Angilletta, M.J.J. (2009) Thermal adaptation: a theoretical and empirical synthesis.
- Arendt, J. (2015) Why get big in the cold? Size–fecundity relationships explain the temperature–size rule in a pulmonate snail (Physa). *Journal of Evolutionary Biology*, 28, 169–178.
- Atkinson, D. (1994) Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research*, 25, 1–58.
- Atkinson, D. (1996) Ectotherm life-history responses to developmental temperature. *Animals and Temperature: Phenotypic and Evolutionary Adaptation*, 1996, 183–204.
- Audzijonyte, A., Barneche, D.R., Baudron, A.R., Belmaker, J., Clark, T.D., Marshall, C.T. et al. (2019) Is oxygen limitation in warming waters a valid mechanism to explain decreased body sizes in aquatic ectotherms? *Ecology and Biogeography*, 28, 64–77.
- Barnett, S. & Dickson, R. (1984) Changes among wild house mice (*Mus musculus*) bred for ten generations in a cold environment, and their evolutionary implications. *Journal of Zoology*, 203, 163–180.
- Bennett, J.M., Sunday, J., Calosi, P., Villalobos, F., Martínez, B., Molina-Venegas, R. et al. (2021) The evolution of critical thermal limits of life on Earth. *Nature Communications*, 12, 1–9.
- Bergmann, C. (1848) Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse.
- Berthold, P., Helbig, A.J., Mohr, G. & Querner, U. (1992) Rapid microevolution of migratory behaviour in a wild bird species. *Nature*, 360, 668–670.
- Borenstein, M., Hedges, L.V., Higgins, J.P. & Rothstein, H.R. (2009) When does it make sense to perform a meta-analysis, Chapter 40. *Introduction to Meta-Analysis*, West Sussex, UK: John Wiley & Sons, pp. 357–364.
- Boyce, M.S. (1984) Restitution of r- and K-selection as a model of density-dependent natural selection. *Annual Review of Ecology and Systematics*, 15, 427–447.
- Cavalheri, H.B., Symons, C.C., Schulhof, M., Jones, N.T. & Shurin, J.B. (2019) Rapid evolution of thermal plasticity in mountain lake *Daphnia* populations. *Oikos*, 128, 692–700.
- Chevin, L.-M., Lande, R. & Mace, G.M. (2010) Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biology*, 8, e1000357.
- Clarke, A. (2003) Costs and consequences of evolutionary temperature adaptation. *Trends in Ecology & Evolution*, 18, 573–581.
- Collins, S. (2011) Competition limits adaptation and productivity in a photosynthetic alga at elevated CO₂. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 278, 247–255.
- Day, T., Abrams, P.A. & Chase, J.M. (2002) The role of size-specific predation in the evolution and diversification of prey life histories. *Evolution*, 56, 877–887.
- Dayan, T. & Simberloff, D. (2005) Ecological and community-wide character displacement: the next generation. *Ecology Letters*, 8, 875–894.
- De Meester, L., Brans, K.I., Govaert, L., Souffreau, C., Mukherjee, S., Vanvelk, H. et al. (2019) Analysing eco-evolutionary dynamics—The challenging complexity of the real world. *Functional Ecology*, 33, 43–59.
- Endler, J.A. (1980) Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, 34, 76–91.
- Endler, J.A. (1986) *Natural selection in the wild*. Princeton, NJ: Princeton University Press.
- Englund, G., Sarnelle, O. & Cooper, S.D. (1999) The importance of data-selection criteria: meta-analyses of stream predation experiments. *Ecology*, 80, 1132–1141.
- Franks, S.J., Sim, S. & Weis, A.E. (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences*, 104, 1278–1282.
- Fussmann, G.F., Loreau, M. & Abrams, P.A. (2007) Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology*, 21, 465–477.
- Futuyma, D.J. (1970) Variation in genetic response to interspecific competition in laboratory populations of *Drosophila*. *American Naturalist*, 104, 239–252.
- Gadgil, M. & Bossert, W.H. (1970) Life historical consequences of natural selection. *American Naturalist*, 104, 1–24.
- Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. & Heinsohn, R. (2011) Declining body size: a third universal response to warming? *Trends in Ecology & Evolution*, 26, 285–291.
- Germain, R.M., Srivastava, D. & Angert, A.L. (2020) Evolution of an inferior competitor increases resistance to biological invasion. *Nature Ecology & Evolution*, 4, 419–425.
- Germain, R.M., Williams, J.L., Schluter, D. & Angert, A.L. (2018) Moving character displacement beyond characters using contemporary coexistence theory. *Trends in Ecology & Evolution*, 33, 74–84.
- Gienapp, P., Teplitsky, C., Alho, J., Mills, J. & Merilä, J. (2008) Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology*, 17, 167–178.
- Grainger, T. & Levine, J. (2021) Data from: Rapid evolution of life history traits in response to warming, predation and competition: a meta-analysis. *Dryad Digital Repository*. Available at: <https://doi.org/10.5061/dryad.xgxd254hh>
- Grainger, T.N., Rudman, S.M., Schmidt, P. & Levine, J.M. (2021) Competitive history shapes rapid evolution in a seasonal climate. *Proceedings of the National Academy of Sciences*, 118(6), e2015772118. <https://doi.org/10.1073/pnas.2015772118>
- Grant, P.R. & Grant, B.R. (2006) Evolution of character displacement in Darwin's finches. *Science*, 313, 224–226.
- Hairston, N.G. Jr, Ellner, S.P., Geber, M.A., Yoshida, T. & Fox, J.A. (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters*, 8, 1114–1127.
- Hargreaves, A.L., Germain, R.M., Bontrager, M., Persi, J. & Angert, A.L. (2020) Local adaptation to biotic interactions: a meta-analysis across latitudes. *American Naturalist*, 195, 395–411.
- Hart, S.P., Turcotte, M.M. & Levine, J.M. (2019) Effects of rapid evolution on species coexistence. *Proceedings of the National Academy of Sciences*, 116, 2112–2117.

- Hendry, A.P. (2019) A critique for eco-evolutionary dynamics. *Functional Ecology*, 33, 84–94.
- Hendry, A.P. & Kinnison, M.T. (1999) Perspective: the pace of modern life: measuring rates of contemporary microevolution. *Evolution*, 53, 1637–1653.
- Hoeksema, J.D., Chaudhary, V.B., Gehring, C.A., Johnson, N.C., Karst, J., Koide, R.T. et al. (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters*, 13, 394–407.
- Holt, B.G. & Jönsson, K.A. (2014) Reconciling hierarchical taxonomy with molecular phylogenies. *Systematic Biology*, 63, 1010–1017.
- Hozo, S.P., Djulbegovic, B. & Hozo, I. (2005) Estimating the mean and variance from the median, range, and the size of a sample. *BMC Medical Research Methodology*, 5(1), 1–10.
- Irschick, D.J. (2003) Measuring performance in nature: implications for studies of fitness within populations. *Integrative and Comparative Biology*, 43, 396–407.
- Jump, A.S. & Penuelas, J. (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, 8, 1010–1020.
- Kambach, S., Bruelheide, H., Gerstner, K., Gurevitch, J., Beckmann, M. & Seppelt, R. (2020) Consequences of multiple imputation of missing standard deviations and sample sizes in meta-analysis. *Ecology and Evolution*, 10, 11699–11712.
- Kawecki, T.J., Lenski, R.E., Ebert, D., Hollis, B., Olivieri, I. & Whitlock, M.C. (2012) Experimental evolution. *Trends in Ecology & Evolution*, 27, 547–560.
- Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E. et al. (2001) The strength of phenotypic selection in natural populations. *American Naturalist*, 157, 245–261.
- Kingsolver, J.G. & Huey, R.B. (2008) Size, temperature, and fitness: three rules. *Evolutionary Ecology Research*, 10, 251–268.
- Lawrence, D., Fiegna, F., Behrends, V., Bundy, J.G., Phillimore, A.B., Bell, T. et al. (2012) Species interactions alter evolutionary responses to a novel environment. *PLoS Biology*, 10, e1001330. <https://doi.org/10.1371/journal.pbio.1001330>.
- McGaughan, A., Laver, R. & Fraser, C. (2021) Evolutionary responses to warming. *Trends in Ecology & Evolution*, 36(7), 591–600. <https://doi.org/10.1016/j.tree.2021.02.014>
- Mueller, L.D. & Ayala, F.J. (1981) Trade-off between r-selection and K-selection in *Drosophila* populations. *Proceedings of the National Academy of Sciences*, 78, 1303–1305.
- Osmond, M.M. & de Mazancourt, C. (2013) How competition affects evolutionary rescue. *Philosophical Transactions of the Royal Society B*, 368, 20120085.
- Palmer, A.R. (1999) Detecting publication bias in meta-analyses: a case study of fluctuating asymmetry and sexual selection. *American Naturalist*, 154, 220–233.
- Parker, G.A. & Begon, M. (1986) Optimal egg size and clutch size: effects of environment and maternal phenotype. *The American Naturalist*, 128, 573–592.
- Partridge, L. & Coyne, J.A. (1997) Bergmann's rule in ectotherms: is it adaptive? *Evolution*, 51(2), 632–635. <https://doi.org/10.1111/j.1558-5646.1997.tb02454.x>
- Partridge, L. & French, V. (1996) Thermal evolution of ectotherm body size: why get big in the cold. *Animals and Temperature: Phenotypic and Evolutionary Adaptation*, 59, 265.
- Pianka, E.R. (1970) On r- and K-selection. *American Naturalist*, 104, 592–597.
- Radchuk, V., Reed, T., Borràs, A., Senar, J.C. & Kramer-Schadt, S. (2019) Adaptive responses of animals to climate change are most likely insufficient.
- Réale, D., McAdam, A.G., Boutin, S. & Berteaux, D. (2003) Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270, 591–596.
- Reznick, D.N., Bassar, R.D., Handelsman, C.A., Ghalambor, C.K., Arendt, J., Coulson, T. et al. (2019) Eco-evolutionary feedbacks predict the time course of rapid life-history evolution. *The American Naturalist*, 194, 671–692.
- Reznick, D.N. & Ghalambor, C.K. (2005) Selection in nature: experimental manipulations of natural populations. *Integrative and Comparative Biology*, 45, 456–462.
- Reznick, D.N., Losos, J. & Travis, J. (2019) From low to high gear: there has been a paradigm shift in our understanding of evolution. *Ecology Letters*, 22, 233–244.
- Reznick, D.N., Shaw, F.H., Rodd, F.H. & Shaw, R.G. (1997) Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science*, 275, 1934–1937.
- Roff, D.A. (2002) *Life history evolution*. Sunderland, USA: Sinauer Associates.
- Rohatgi, A. (2020) WebPlotDigitizer. <https://automeris.io/WebPlotDigitizer>, Pacifica, California, USA.
- Rudman, S.M., Barbour, M.A., Csilléry, K., Gienapp, P., Guillaume, F., Hairston Jr, N.G. et al. (2018) What genomic data can reveal about eco-evolutionary dynamics. *Nature Ecology & Evolution*, 2, 9–15.
- Rudman, S.M., Greenblum, S.I., Rajpurohit, S., Betancourt, N.J., Hanna, J., Tilk, S., et al. (2021). Direct observation of adaptive tracking on ecological timescales in *Drosophila*. *bioRxiv*. <https://doi.org/10.1101/2021.04.27.441526>
- Santos, M., Borash, D.J., Joshi, A., Bounlutay, N. & Mueller, L.D. (1997) Density-dependent natural selection in *Drosophila*: evolution of growth rate and body size. *Evolution*, 51, 420–432.
- Schaffer, W. & Gadgil, M.D. (1975) Selection for optimal life histories in plants. In: Cody, M.L., MacArthur, R.H. & Diamond, J.M. (Eds.) *Ecology and evolution of communities*. USA: Harvard University Press Cambridge, pp. 142–157.
- Schluter, D. & McPhail, J.D. (1992) Ecological character displacement and speciation in sticklebacks. *American Naturalist*, 140, 85–108.
- Sheridan, J.A. & Bickford, D. (2011) Shrinking body size as an ecological response to climate change. *Nature Climate Change*, 1, 401–406.
- Siepielski, A.M., Morrissey, M.B., Carlson, S.M., Francis, C.D., Kingsolver, J.G., Whitney, K.D. et al. (2019) No evidence that warmer temperatures are associated with selection for smaller body sizes. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 286, 20191332.
- Stearns, S.C. (1983) A natural experiment in life-history evolution: field data on the introduction of mosquitofish (*Gambusia affinis*) to Hawaii. *Evolution*, 37, 601–617.
- Stearns, S.C. (1989) Trade-offs in life-history evolution. *Functional Ecology*, 3, 259–268.
- Taylor, B.E. & Gabriel, W. (1992) To grow or not to grow: optimal resource allocation for *Daphnia*. *American Naturalist*, 139, 248–266.
- Teplitsky, C. & Millien, V. (2014) Climate warming and Bergmann's rule through time: is there any evidence? *Evolutionary Applications*, 7, 156–168.
- TerHorst, C. (2011) Experimental evolution of protozoan traits in response to interspecific competition. *Journal of Evolutionary Biology*, 24, 36–46.
- Terhorst, C.P. (2010) Evolution in response to direct and indirect ecological effects in pitcher plant inquiline communities. *American Naturalist*, 176, 675–685.
- Terhorst, C.P., Miller, T.E. & Levitan, D.R. (2010) Evolution of prey in ecological time reduces the effect size of predators in experimental microcosms. *Ecology*, 91, 629–636.
- Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends in Ecology & Evolution*, 13, 329–332.
- Tobler, R., Hermisson, J. & Schlötterer, C. (2015) Parallel trait adaptation across opposing thermal environments in experimental *Drosophila melanogaster* populations. *Evolution*, 69, 1745–1759.

- Tseng, M., Bernhardt, J.R. & Chila, A.E. (2019) Species interactions mediate thermal evolution. *Evolutionary Applications*, 12, 1463–1474.
- Tseng, M. & O'Connor, M. (2015) Predators modify the evolutionary response of prey to temperature change. *Biology Letters*, 11, 20150798.
- Urban, M.C. (2007) The growth–predation risk trade-off under a growing gape-limited predation threat. *Ecology*, 88, 2587–2597.
- Van Doorslaer, W., Stoks, R., Jeppesen, E. & De Meester, L. (2007) Adaptive microevolutionary responses to simulated global warming in *Simocephalus vetulus*: a mesocosm study. *Global Change Biology*, 13, 878–886.
- Watt, C., Mitchell, S. & Salewski, V. (2010) Bergmann's rule; a concept cluster? *Oikos*, 119, 89–100.
- Williams, C.K. & Moore, R. (1989) Phenotypic adaptation and natural selection in the wild rabbit, *Oryctolagus cuniculus*, Australia. *The Journal of Animal Ecology*, 58(2), 495–507. <https://doi.org/10.2307/4844>
- Wright, J., Bolstad, G.H., Araya-Ajoy, Y.G. & Dingemans, N.J. (2019) Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. *Biological Reviews*, 94, 230–247.
- Yamamichi, M., Yoshida, T. & Sasaki, A. (2011) Comparing the effects of rapid evolution and phenotypic plasticity on predator-prey dynamics. *The American Naturalist*, 178, 287–304.
- Yampolsky, L.Y. & Scheiner, S.M. (1996) Why larger offspring at lower temperatures? A demographic approach. *American Naturalist*, 147, 86–100.

STUDIES INCLUDED IN THE DATASET AND NOT CITED ELSEWHERE

- Alzate, A., Bisschop, K., Etienne, R.S. & Bonte, D. (2017) Interspecific competition counteracts negative effects of dispersal on adaptation of an arthropod herbivore to a new host. *Journal of Evolutionary Biology*, 30, 1966–1977.
- Anderson, W.W. (1966) Genetic divergence in *M. Vetukhiv's* experimental populations of *Drosophila pseudoobscura* 3. *Divergence in Body Size. Genetics Research*, 7, 255–266.
- Berger, D., Walters, R.J. & Blanckenhorn, W.U. (2014) Experimental evolution for generalists and specialists reveals multivariate genetic constraints on thermal reaction norms. *Journal of Evolutionary Biology*, 27, 1975–1989.
- Berven, K.A., Gill, D.E. & Smith-Gill, S.J. (1979) Countergradient selection in the green frog. *Rana clamitans*. *Evolution*, 609–623.
- Bisschop, K., Mortier, F., Bonte, D. & Etienne, R.S. (2020) Performance in a novel environment subject to ghost competition. *PeerJ*, 8, e8931.
- Bochdanovits, Z. & Jong, G.D. (2003) Experimental evolution in *Drosophila melanogaster*: interaction of temperature and food quality selection regimes. *Evolution*, 57, 1829–1836.
- Breckels, R.D., Garner, S.R. & Neff, B.D. (2014) Rapid evolution in response to increased temperature maintains population viability despite genetic erosion in a tropical ectotherm. *Evolutionary Ecology*, 28, 141–155.
- Bryant, E.H. & Turner, C.R. (1972) Rapid evolution of competitive ability in larval mixtures of the housefly. *Evolution*, 161–170.
- Cavicchi, S., Guerra, D., Giorgi, G. & Pezzoli, C. (1985) Temperature-related divergence in experimental populations of *Drosophila melanogaster*. I. Genetic and developmental basis of wing size and shape variation. *Genetics*, 109, 665–689.
- Chapuis, E., Lamy, T., Pointier, J.-P., Juillet, N., Ségard, A., Jarne, P. et al. (2017) Bioinvasion triggers rapid evolution of life histories in freshwater snails. *The American Naturalist*, 190, 694–706.
- De Meester, L., Boersma, M. & Spaak, P. (1999) Environmental stress and local adaptation in *Daphnia magna*. *Limnology and Oceanography*, 44, 393–402.
- Downhower, J.F., Brown, L.P. & Matsui, M.L. (2000) Life history variation in female *Gambusia hubbsi*. *Environmental Biology of Fishes*, 59, 415–428.
- Fisk, D.L., Latta, L.C., Knapp, R.A. & Pfrender, M.E. (2007) Rapid evolution in response to introduced predators I: rates and patterns of morphological and life-history trait divergence. *BMC Evolutionary Biology*, 7, 1–11.
- Fryxell, D.C., Hoover, A.N., Alvarez, D.A., Arnesen, F.J., Benavente, J.N., Moffett, E.R. et al. (2020) Recent warming reduces the reproductive advantage of large size and contributes to evolutionary downsizing in nature. *Proceedings of the Royal Society B*, 287, 20200608.
- Geerts, A., Vanoverbeke, J., Vanschoenwinkel, B., Van Doorslaer, W., Feuchtmayr, H., Atkinson, D. et al. (2015) Rapid evolution of thermal tolerance in the water flea *Daphnia*. *Nature Climate Change*, 5, 665–668.
- Hausch, S.J., Vamosi, S.M. & Fox, J.W. (2020) Experimental evolution of competing bean beetle species reveals long-term reversals of short-term evolution, but no consistent character displacement. *Ecology and Evolution*, 10, 3727–3737.
- Hendry, A.P., Hensleigh, J.E. & Reisenbichler, R.R. (1998) Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington. *Canadian Journal of Fisheries and Aquatic Science*, 55, 1387–1394.
- James, A.C. & Partridge, L. (1995) Thermal evolution of rate of larval development in *Drosophila melanogaster* in laboratory and field populations. *Journal of Evolutionary Biology*, 8, 315–330.
- Latta, L.C., Bakelar, J.W., Knapp, R.A. & Pfrender, M.E. (2007) Rapid evolution in response to introduced predators II: the contribution of adaptive plasticity. *BMC Evolutionary Biology*, 7, 1–9.
- Leibold, M. & Tessier, A.J. (1991) Contrasting patterns of body size for *Daphnia* species that segregate by habitat. *Oecologia*, 86, 342–348.
- Nunes, A.L., Orizaola, G., Laurila, A. & Rebelo, R. (2014) Rapid evolution of constitutive and inducible defenses against an invasive predator. *Ecology*, 95, 1520–1530.
- Parejko, K. & Dodson, S.I. (1991) The evolutionary ecology of an antipredator reaction norm: *daphnia pulex* and *Chaoborus Americanus*. *Evolution*, 45, 1665–1674.
- Partridge, L., Barrie, B., Barton, N.H., Fowler, K. & French, V. (1995) Rapid laboratory evolution of adult life-history traits in *Drosophila melanogaster* in response to temperature. *Evolution*, 49, 538–544.
- Partridge, L., Barrie, B., Fowler, K. & French, V. (1994) Evolution and development of body size and cell size in *Drosophila melanogaster* in response to temperature. *Evolution*, 48, 1269–1276.
- Powell, J.R. (1974) Temperature related genetic divergence in *Drosophila* body size. *Journal of Heredity*, 65, 257–258.
- Reznick, D. (1982) The impact of predation on life history evolution in Trinidadian guppies: genetic basis of observed life history patterns. *Evolution*, 36(6), 1236–1250.
- Rogell, B., Widegren, W., Hallsson, L.R., Berger, D., Björklund, M. & Maklakov, A.A. (2014) Sex-dependent evolution of life-history traits following adaptation to climate warming. *Functional Ecology*, 28, 469–478.
- Samuk, K., Xue, J. & Rennison, D.J. (2018) Exposure to predators does not lead to the evolution of larger brains in experimental populations of threespine stickleback. *Evolution*, 72, 916–929.
- Schwarz, R., Itescu, Y., Antonopoulos, A., Gavriilidi, I.-A., Tamar, K., Pafilis, P. et al. (2020) Isolation and predation drive gecko life-history evolution on islands. *Biological Journal of the Linnean Society*, 129, 618–629.
- Sokal, R.R., Bryant, E.H. & Wool, D. (1970) Selection for changes in genetic facilitation: negative results in *Tribolium* and *Musca*. *Heredity*, 25, 299–306.
- Sparks, M.M., Westley, P.A., Falke, J.A. & Quinn, T.P. (2017) Thermal adaptation and phenotypic plasticity in a warming world: Insights from common garden experiments on Alaskan sockeye salmon. *Global Change Biology*, 23, 5203–5217.
- Spitze, K. (1991) *Chaoborus* predation and life-history evolution in *Daphnia pulex*: temporal pattern of population diversity, fitness, and mean life history. *Evolution*, 45, 82–92.
- Stoks, R., Govaert, L., Pauwels, K., Jansen, B. & De Meester, L. (2016) Resurrecting complexity: the interplay of plasticity and rapid evolution in the multiple trait response to strong changes in predation pressure in the water flea *Daphnia magna*. *Ecology Letters*, 19, 180–190.
- Stuart, Y.E., Campbell, T., Hohenlohe, P., Reynolds, R.G., Revell, L. & Losos, J. (2014) Rapid evolution of a native species following invasion by a congener. *Science*, 346, 463–466.
- Sulzbach, D. & Emlen, J. (1979) Evolution of competitive ability in mixtures of *Drosophila melanogaster*: populations with an initial asymmetry. *Evolution*, 33, 1138–1149.
- Taper, M.L. (1990) Experimental character displacement in the adzuki bean weevil, *Callosobruchus chinensis*. In Fuji, K., Gatehouse, A.M.R., Johnson, C.D., Mitchel, R. & Yoshida, T. (Eds.) *Bruchids and Legumes: economics, ecology and coevolution*. Dordrecht: Kluwer Academic Publishers, pp. 289–301.
- Telemeco, R.S., Radder, R.S., Baird, T.A. & Shine, R. (2010) Thermal effects on reptile reproduction: adaptation and phenotypic plasticity in a montane lizard. *Biological Journal of the Linnean Society*, 100, 642–655.
- Urban, M.C. (2008) Salamander evolution across a latitudinal cline in gape-limited predation risk. *Oikos*, 117, 1037–1049.
- Van Doorslaer, W., Stoks, R., Duvivier, C., Bednarska, A. & De Meester, L. (2009) Population dynamics determine genetic adaptation to temperature

- in *Daphnia*. *Evolution: International Journal of Organic Evolution*, 63, 1867–1878.
- Van Doorslaer, W., Stoks, R., Swillen, I., Feuchtmayr, H., Atkinson, D., Moss, B. et al. (2010) Experimental thermal microevolution in community-embedded *Daphnia* populations. *Climate Research*, 43, 81–89.
- Walczyńska, A., Franch-Gras, L. & Serra, M. (2017) Empirical evidence for fast temperature-dependent body size evolution in rotifers. *Hydrobiologia*, 796, 191–200.
- Walsh, M.R. & Reznick, D.N. (2008) Interactions between the direct and indirect effects of predators determine life history evolution in a killifish. *Proceedings of the National Academy of Sciences*, 105, 594–599.
- Walsh, M.R. & Reznick, D.N. (2010) Influence of the indirect effects of guppies on life-history evolution in *Rivulus hartii*. *Evolution*, 64, 1583–1593.
- Wathne, I., Enberg, K., Jensen, K.H. & Heino, M. (2020) Rapid life-history evolution in a wild *Daphnia pulex* population in response to novel size-dependent predation. *Evolutionary Ecology*, 34, 257–271.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Grainger, T.N. & Levine, J.M. (2021) Rapid evolution of life-history traits in response to warming, predation and competition: A meta-analysis. *Ecology Letters*, 00, 1–14.
Available from: <https://doi.org/10.1111/ele.13934>