ECOLOGY LETTERS

Ecology Letters, (2020) **23**: 951–961 doi: 10.1111/ele.13491

LETTER

Predators weaken prey intraspecific competition through phenotypic selection

Adam M. Siepielski,* Adam Z. Hasik, Taylor Ping, Mabel Serrano, Koby Strayhorn and Simon P. Tye

Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA

**Correspondence: Email: amsiepie@uark.edu*

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13491

Abstract

Predators have a key role shaping competitor dynamics in food webs. Perhaps the most obvious way this occurs is when predators reduce competitor densities. However, consumption could also generate phenotypic selection on prey that determines the strength of competition, thus coupling consumptive and trait-based effects of predators. In a mesocosm experiment simulating fish predation on damselflies, we found that selection against high damselfly activity rates – a phenotype mediating predation and competition – weakened the strength of density dependence in damselfly growth rates. A field experiment corroborated this finding and showed that increasing damselfly densities in lakes with high fish densities had limited effects on damselfly growth rates but generated a precipitous growth rate decline where fish densities were lower – a pattern expected because of spatial variation in selection imposed by predation. These results suggest that accounting for both consumption and selection is necessary to determine how predators regulate prey competitive interactions.

Keywords

Adaptation, competition, density dependence, eco-evo, food web, predation, selection.

Ecology Letters (2020) **23**: 951–961

INTRODUCTION

Considerable work has shown that predators can directly and indirectly influence the strength of density dependence in prey competitive interactions. Direct, density-mediated effects occur when predators reduce the abundance of their prey, thus weakening competition (Paine 1966; Chase *et al.* 2002; Chesson & Kuang 2008). Indirect, trait-mediated effects occur when predators illicit trait changes in a prey species that have cascading effects on competitor demographic rates (Peacor & Werner 2001). This body of work has mainly focused on plasticity and behaviourally mediated trait changes (Abrams 1984; Beckerman *et al.* 1997; Werner & Peacor 2003; Schmitz *et al.* 2004; Preisser *et al.* 2005; Sommers & Chesson 2019). However, inferences concerning such trait-mediated effects are, by necessity, made by masking the direct consumptive effects of predators. While insightful, this approach precludes an understanding of the effects of phenotypic selection by predators in regulating competition (Kratina *et al.* 2010; Hammill *et al.* 2015). Yet predation is a driving selective force of prey populations (Endler 1986; Ruxton *et al.* 2004; Benkman 2013), and may be critical in shaping the ecological dynamics of how competitor density dependence operates (Travis *et al.* 2013; McPeek 2017a).

The effects of selection by predators on intraspecific competition can arise because the traits that mediate competition can trade-off with the risk of predation. For example, higher activity levels and foraging rates might allow prey to usurp more resources and be a superior competitor, but it comes at the cost of increased mortality by predators (Lima & Dill 1990; Lima 1998). Although the well-studied growth-predation tradeoff underlies this argument (Sih 1987; Werner & Anholt 1993; McNamara & Houston 1994; McPeek 2004; Urban 2007a), work has only recently begun to incorporate the role that intraspecific phenotypic variation in activity plays in mediating such interactions (Brodin & Johansson 2004; Stamps 2007; Urban 2007b; Bolnick *et al.* 2011; Start & Gilbert 2017). This is important to consider because decades of work on predator driven selection demonstrates that individuals consumed by predators are typically not a random subset of populations (Ruxton *et al.* 2004). Collectively, these findings allude to an untested hypothesis: that selection on prey activity by predators shapes the strength of density dependence underlying intraspecific competition in prey.

Here, we take an experimental approach to test this latter hypothesis. We develop a system to capture the interactions between fish predators and one of their prey, larval damselflies. We first conducted a phenotypic selection experiment to generate contrasting distributions of damselfly activity levels that would result from varying strengths of directional selection imposed by fish. We then manipulated damselfly densities in these activity level distributions to understand how intraspecific competition may be affected by selection on activity. Our previous work found that the strength of selection on damselfly activity varies with fish densities (Ousterhout *et al.* 2018), as the strength of selection on prey is expected to increase with prey mortality (Benkman 2013). It follows then, that as fish densities increase, stronger selection for reduced activity should weaken the strength of intraspecific competition in the wild. To test this idea, we conducted a field experiment where we manipulated damselfly densities across lakes varying in fish densities.

METHODS

Study system

We focused on predator-prey interactions between centrarchid fish and larvae of the orange bluet (*Enallagma signatum*), a common damselfly found in our Northwestern Arkansas study region. *Enallagma* are mid-trophic level ambush predators found in many lakes, where the larvae inhabit macrophytes, feed on smaller invertebrates, and are fed upon by themselves and larger predators, especially fish (McPeek 1990; McPeek 1998; McPeek & Brown 2000; Ousterhout *et al.* 2018). Fish predation has repeatedly been shown to select for reduced activity levels in damselflies (Strobbe *et al.* 2011; Swaegers *et al.* 2017; Ousterhout *et al.* 2018). Selection operates in this stereotypical way because damselflies attract fish when swimming (Baker *et al.* 1999) and cannot swim away fast enough to evade fish (McPeek 2000; Stoks & De Block 2000); therefore reducing activity helps damselflies avoid detection (Strobbe *et al.* 2011).

In addition to this well-established predator-prey relationship, damselflies are an ideal study system to test our hypothesis because they engage in both indirect exploitative and direct interference competition – experimentally increasing their densities reduces growth rates (Anholt 1990; McPeek 1990; McPeek 1998; McPeek & Brown 2000; Siepielski *et al.* 2010). Growth rates are a key fitness component for damselflies (Brodin & Johansson 2004) and many species in general (Urban 2007a). For instance, growth rates determine the duration that damselfly larvae are exposed to predators (McPeek & Peckarsky 1998), and damselflies are only able to reproduce if they metamorphose. Importantly, previous food addition field experiments have shown that damselfly growth rates are food limited, implying a role for indirect resource competition (McPeek 1998) and direct competition via feeding interference (McPeek & Crowley 1987). Encounters between damselflies also result in aggressive interactions (Baker 1981; McPeek & Crowley 1987), sometimes leading to cannibalism of smaller individuals (Johnson 1991; Anholt 1994). This threat of cannibalism generates a strong stress response that can reduce growth rates by upwards of 50% when conspecifics are present (McPeek *et al.* 2001), and higher activity rates increase such encounters (Start *et al.* 2017).

Behavioural assays to quantify activity rate phenotypes in damselflies

To obtain a large range of variation in damselfly activity phenotypes, which is required to detect selection, we used D-frame dipnets (28-cm opening, 1 × 1 mm mesh) to gather late instar *E. signatum* from two lakes, Charleston and Greenwood, located in west-central AR, USA. Prior sampling of these lakes indicated they had very low fish densities (1.08 and 1.18 fish/m^2, Charleston and Greenwood respectively; Ousterhout *et al.* 2019). Although some selection likely occurred prior to sampling (Steele *et al.* 2011), meaning that very active individuals may be underrepresented, low fish densities generate relatively weak selection against damselfly activity levels (Ousterhout *et al.* 2018) which allowed us to obtain substantial variation in activity levels.

We quantified activity phenotypes using an open fields test that has previously been used to quantify these attributes in odonates (Johansson & Rowe 1999; Brodin & Johansson 2004; Start & Gilbert 2017). All assays were performed under natural lighting conditions in a greenhouse. We conducted assays on 400 individuals by placing single larvae in petri dishes (10-cm diameter) filled with filtered lake water. Although this arena simplifies the environment (e.g. no habitat structure allowing vertical movements, no predator cues), these assays provide a repeatable measure of activity (Start & Gilbert 2017; Start 2018, and below). All individuals were allowed to acclimate to these conditions for 12–15 h, and in the absence of food to standardise hunger levels which could affect their motivation for movement, before we began recording the position of each individual every 20 min for 3 h. The sum of the minimum distances between successive locations over the assay period was used as a measure of activity rate, expressed as mm moved/3 h. To examine if this phenotype was a repeatable trait, we repeated this assay on 30 additional larvae separated by a 3-week period; repeatability was high (intraclass correlation coefficient = 0.567, 95% CI: 0.270, 0.767).

Although activity phenotypes of damselflies are repeatable, they are also influenced by environmental factors (Johansson 1993; McPeek 2004; Brodin 2009). In particular, many studies have shown that in the presence of fish cues (olfactory and visual), damselfly activity levels decline (McPeek 2004; Siepielski *et al.* 2016). Consistent with previous studies we also found that activity rates declined in the presence of fish cues (by ~26%; Appendix S1); however, activity rates among individuals were consistent in the presence or absence of these cues (Fig. S1; see also Start 2018). Since the activity rate data used for subsequent experiments was collected in the absence of fish cues, our estimates of activity levels, attack rates and handling times (see below), are likely higher than those in the presence of fish cues naturally occurring in lakes, though this should not affect our qualitative interpretations.

Experimentally imposing phenotypic selection on damselfly activity rates

From numerous studies of selection by fish on *Enallagma* damselflies we know fish predation consistently generates directional selection reducing mean activity levels within populations (Strobbe *et al.* 2011; Swaegers *et al.* 2017; Ousterhout *et al.* 2018). We therefore capitalised on our detailed knowledge of this study system and implemented a phenotypic selection experiment on damselfly activity phenotypes that created differences in the intensity of selection (e.g. simulating differences in mean activity levels before and after predation by fish).

We imposed selection on activity phenotypes by first ranking the 400 individuals we assayed above on the basis of their activity rates (Fig. 1 grey bars), and then split this overall distribution into four different selection levels ($n = 85$ individuals/selection level) that corresponded with different mean activity rates (different coloured bars in Fig. 1, Fig. S2). Each "selected" group therefore corresponded with a different intensity of selection, from favouring active to less active individuals on average relative to the initial distribution. These differences are representative of population-level variation in activity levels of odonates (Start 2018) and should reflect differences in survivorship across fish densities (Ousterhout *et al.* 2018).

Although we assayed 400 individuals, we only used 340 individuals in the subsequent experiment manipulating densities and for our estimates of foraging traits (see below). The 60 individuals not used were from the portion of activity rate distribution

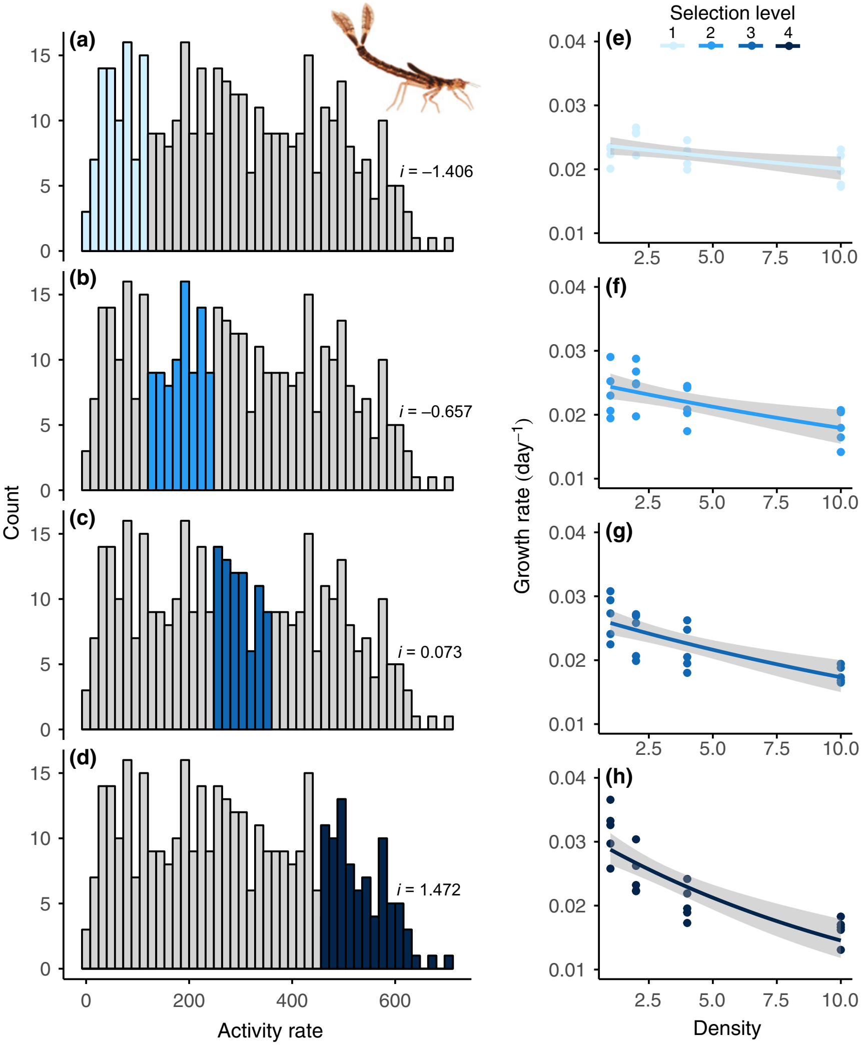

Figure 1 Selection shifting from favouring less active to more active individuals caused the strength of density dependence in damselfly growth rates to increase. (a–d) Distribution of activity phenotypes (activity rate: distance in mm moved per 3 h). Grey bars denote the entire distribution of activity rates, and colours correspond to the distribution of activity rates resulting from different levels of selection generated in the mesocosm experiment. The strength and direction of selection are denoted by the standardised selection differentials *i*, which are corrected for size. From (a–d), the selection experiment generated more active individuals on average. (e–f) The relationship between growth rates and damselfly density for a given selection level. Lines denote the log-linear regression and grey bands denote 95% CI. Model parameter estimates can be found in Table S1. Picture of *E. signatum* provided by S. Krotzer.

between the third and fourth selection groups, so that the fourth selection group included the most active individuals (Fig. 1). As a measure of selection, we present standardised selection differentials (i; or selection intensities), quantified as the difference in mean activity rates between the selected individuals in a group (μ_s) and the entire distribution (μ) relative to the combined standard deviation (σ), $i = (\mu_s - \mu)/\sigma$. Because activity levels were weakly positively correlated with size (regression of activity against head width gave an adj. $R^2 = 10.2\%$, Fig. S3), we used the residuals from a regression of head width and activity rate as a measure of size corrected activity rates.

Mesocosm experiment to investigate how selection mediates the strength of density dependence in growth rates

To isolate the relative effects of density (i.e. consumption by fish reducing damselfly density) and selective trait-mediated effects of predation (i.e. selection favouring less active individuals) on the strength of competition, we conducted a density manipulation experiment crossed with the four different levels of selection intensities generated in our selection experiment. This crossed-design therefore allowed us to understand the potential roles of fish predation depressing damselfly densities relative to the effect of selection on activity levels. The interaction between these two factors captures how differential survival among individuals with varying activity levels affects the strength of intraspecific competition.

We established 5.5 L mesocosms (0.25 m diameter, bottom area of 0.05m^2) in a greenhouse with filtered lake water (as an algae source; 0.77 mm mesh), macrophytes (*Ceratophyllum* spp.), and *Daphnia* as a prey item. *Daphnia* were established at ~50 individuals/L. Damselfly densities were established at 1, 2, 4 and 10 individuals per mesocosm producing densities between ~20 and 198 damselflies/m^2. These densities bracket the ranges typical of our study region (mean = 132 *Enallagma*/m^2 ± 141 SD; range 32–205; Ousterhout *et al.* 2019), and should be sufficient to detect density-dependent growth (McPeek 1990; McPeek 1998; Siepielski *et al.* 2010; Siepielski *et al.* 2016b). Each of the four selection levels was crossed with the four density levels with five replicates per combination (n = 80 total mesocosms).

As in previous studies (McPeek 1990; McPeek 1998; Siepielski *et al.* 2010; Bried & Siepielski 2019), mean growth rates were calculated for each mesocosm separately and used as the response variable in statistical analyses. This methodology was employed, because with the exception of the single density treatment, we cannot identify individuals (damselflies grow by molting). Growth rates were calculated as [mean(ln(head width of recovered larvae)) – mean(ln(head width of initial sample))]/duration. This growth rate metric assumes a model of head width(t) = head width(0)e$^{(gt)}$, where t is the time interval and g the growth rate (McPeek 1998). Head widths were measured from photographs with ImageJ (v. 2.0, Rueden *et al.*2017). The time interval used, 21 days, is sufficient to detect growth rates (McPeek 2004; Siepielski *et al.* 2010).

Quantifying attack rates and handling times in response to selection

To investigate mechanistically what might underlie changes in activity-mediated growth rates in response to selection, we estimated damselfly attack rates and handling times after the behavioural assays using the protocol established by Villalobos-Jiménez *et al.* (2017). In brief, we starved each larva for an additional 24 h period to ensure motivation for feeding and standardise hunger levels, then introduced different densities of *Daphnia magna* (2, 4, 8, 16, or 32) to the petri dishes. *Daphnia* were standardised to a uniform size by passing them through mesh sieves with perforations between 0.84 and 1.00 mm. After *Daphnia* were introduced, damselflies were allowed to feed for 20 h and the number of remaining *Daphnia* counted. Since prey were not replaced during the experiment, we estimated attack rate and handling time using Rogers' type II functional response formulae (Rogers 1972):

$$N_a = N_o\left(1 - e^{-a(T - h\times N_a}\right) \quad (1)$$

where N_a is the number of prey consumed, N_o prey density, T total time prey were exposed to predation, a attack rate, and h handling time, as implemented in the frair package (Pritchard *et al.* 2017). These parameters were estimated for each selection level separately.

Activity rates and density-dependent growth along a gradient of fish and prey densities

Previous experimental work has established that the strength of directional selection favouring reduced activity in damselflies increases with fish density (Ousterhout *et al.* 2018). Previous studies have also shown that damselfly growth rates (Shama *et al.* 2011) and activity associated behaviours (Swaegers *et al.* 2017) are heritable. Thus, if damselflies differentially adapt to inhabiting lakes with greater fish densities their activity levels should decline as fish densities increase. Such evolution should also manifest as reductions in maximal growth rates and the strength of density dependence in growth rates with increasing fish densities. Previous surveys in our region found that densities of the dominant predator, bluegill (*Lepomis macrochirus*), vary among lakes (Ousterhout *et al.* 2019), which allowed us to examine how activity levels and the strength of density dependence varied with fish densities under field conditions. We also examined how prey density could affect growth rates, since damselfly growth is prey limited (McPeek 1998), and prey densities vary among lakes (Ousterhout *et al.* 2019).

During April – May 2019, we established 20 submerged cages (0.23 m high × 0.23 m wide × 0.23 m long; bottom surface area of 0.052 m^2) in the littoral zone of each of six lakes with varying bluegill densities (Ousterhout *et al.* 2019) (Range among lakes = ~1–16 mean fish/m^2; based on three seine hauls; Fig. 3; Table S2). Prey densities on submerged macrophytes (where damselflies forage) were estimated by taking six replicate samples with a 6 L box sampler (100-µm mesh) at each lake (see Siepielski *et al.* 2010; Ousterhout *et al.* 2019). Prey densities among lakes ranged between ~12 and 121 prey/6L (Fig. 3; Table S2).

Cages were constructed of PVC pipe (2.1 cm diameter) encased in mesh netting (0.6 × 1.2 mm mesh), which allowed prey to colonise cages and excluded other competitors. To provide a foraging structure for damselflies, we added the dominant macrophyte (*Justicia americana*) at natural densities to each cage. All damselflies were from their local lakes and included the natural size variation present in each lake at the time the experiments were established. We used the same damselfly densities (1, 2, 4 or 10 per cage; 4–5 replicates per treatment), methodology for estimating growth rates (using means per cage), and experimental duration as described above. Initial head widths were measured from a subset of larvae not used when stocking cages.

To quantify activity rates among lakes, we gathered 20–30 damselflies in each of the same six lakes we established experimental cages in. We then used the same behavioural assay as described above to estimate activity rates.

Statistical analysis

To first confirm that the phenotypic selection experiment generated differences in mean activity rates we used a general linear model (GLM) of the form: activity rate as the response, with selection level as the explanatory factor. As with the estimates of selection differentials, we used the residuals from a regression of activity and head width as a measure of size corrected activity rate since activity rates were weakly positively correlated with size (Fig. S3).

Our primary question in the mesocosm experiment was to examine if differences in selection on activity rates affected the strength of density-dependent growth in damselflies. We therefore used a GLM of the form: log(growth rates) as the response variable with damselfly density and selection level, and their interaction as explanatory factors (Table S1). A log-linear model was chosen because growth rates as a function of density revealed a non-linear pattern that declined rapidly with increased density (Fig. 1), and AIC model comparisons indicated these models had lower AIC scores. Although selection levels were treated categorically, they reflected differences in mean activity rates (e.g. Fig. S2). For this model, a significant interaction would indicate that the effect of damselfly density on growth rates depended on the selection level.

Differences in growth rates originating from selection could arise through a number of mechanisms, including how differences in selection on activity affect damselfly attack rates and handling times. To determine if the experimental selection we imposed influenced attack rates and handling times, we used the "frair_compare" function in the *frair* package (Pritchard *et al.* 2017). This approach is widely used in functional response studies (Villalobos-Jiménez *et al.* 2017) and implements an indicator analysis (Juliano *et al.* 2001) to test the null hypothesis that a and h for a given comparison are equivalent.

Our second question was whether differences in fish and prey densities among lakes, which were not correlated ($n = 6$, $r = 0.148$, $P = 0.780$), could affect the strength of density dependence in damselfly growth rates. To examine this, we built a GLM of the form: log(growth rate) as the response variable, with damselfly density, fish density, prey density and interactions between damselfly density and fish or prey density, as explanatory factors (Table 1). For this experiment, we had mortality from unknown causes (cannibalism is possible, but mortality occurred across all densities), as well as several treatments or replicates where cages were lost due to intense spring storms, including the entire single individual density treatment at Lake Fayetteville, which may have affected our estimate of maximal growth rates. Because it was impossible to determine when individuals died, we used initial densities.

To examine if activity rates were associated with fish densities, we use a GLM of the form activity rate as the response variable and fish density as the explanatory factor. Damselfly head width was included as a covariate to take into account potential effects of size.

RESULTS

Effects of experimental selection on activity rates and density-dependent growth rates

Individual damselflies varied considerably in activity rate phenotypes (Fig. 1; Fig. S2) and our phenotypic selection experiment generated differences in average activity rate phenotypes (Fig. S2). The resulting size-corrected selection differentials varied from $i = -1.40$ to 1.47, from the least to most active selection level respectively (Fig. 1a–d).

The effects of damselfly density on growth rate depended on the strength and direction of selection generated in the selection experiment (interaction term: $F_{3,71} = 4.887$, $P = 0.004$, R^2 for whole model = 54.34; Fig. 1e–h; Table S1). While the relative contributions of each of these factors varied, the latter effect revealed that selection shaped the strength of intraspecific competition. The partial adjusted R^2 was 49.35% for damselfly density, 8.58% for the interaction term and 0.5% for the effects of selection on growth rates.

Since the significant interaction term showed that selection affected the strength of density dependence, we conducted individual regressions of log(growth rate) in relation to damselfly density for each selection level. We found that the strength of density dependence on growth rates (the slope) generally weakened as selection for less active individuals increased (Fig. 1; Table S1). As a measure of the effect size for this association, we determined the adj. R^2 from a linear model regressing these slopes against i. The estimated slopes of growth rate in relation to density were well explained by the strength and direction of selection ($R^2 = 86.6\%$).

Effects of experimental selection on damselfly attack rates and handling times

Differences in the strength and direction of selection generated in our selection experiment also produced differences in attack rates and handling times that varied across selection levels (Fig. 2). Attack rates generally declined with selection for less active individuals, but only comparisons between selection for the lowest and highest activity levels were significantly different (Fig. 2e). Handling rates also increased with selection for less active individuals, but only comparisons between the selection level favouring the most active individuals and all other handling times was significant (Fig. 2f). Thus, extremes in selection were necessary to detect changes in functional responses of damselflies to prey.

Density-dependent growth rates along a gradient of fish and prey densities

The effects of damselfly densities on growth rates depended on fish, but not prey densities, among lakes (Fig. 3, Table 1). Therefore, we conducted individual log-linear regressions of growth rates in relation to damselfly density for each lake (Fig. 3, Table S2). We found that the strength of density dependence in growth generally declined as fish densities increased; however, it did so non-linearly and reached an asymptote once fish densities approached ~6 fish/m^2 (Fig. 3b). As a measure of effect size, we extracted the slopes from each individual regression and constructed a weighted regression model (slope = fish density + fish density^2; weighted by 1/SE of the estimated slope) to determine the R^2 of this relationship. The estimated slopes of growth rates in relation to damselfly density relative to fish densities were well explained by this model ($R^2 = 70.67\%$; Fig. 3b). To examine whether fish densities were related to maximal estimated growth rates, we took a similar approach but with the estimated intercepts as a measure of maximal growth. Maximal growth rates were not well explained by fish densities among lakes ($R^2 = 14.7\%$; Fig. 3c).

We also found that the strength of density dependence in damselfly growth rates (the slopes) was not associated with prey density ($R^2 = 16.75\%$; Fig. 3d). However, there was a significant effect of prey density among lakes on overall growth rates (Table 1), and maximal estimated growth rates (intercepts) increased sharply with increasing prey densities ($R^2 = 59.6\%$; Fig. 3e).

Damselfly activity rates along a gradient of fish densities

Although there was variation in activity rates within populations, mean activity rates of damselflies declined with increases in fish densities (Fig. 4, Table S3).

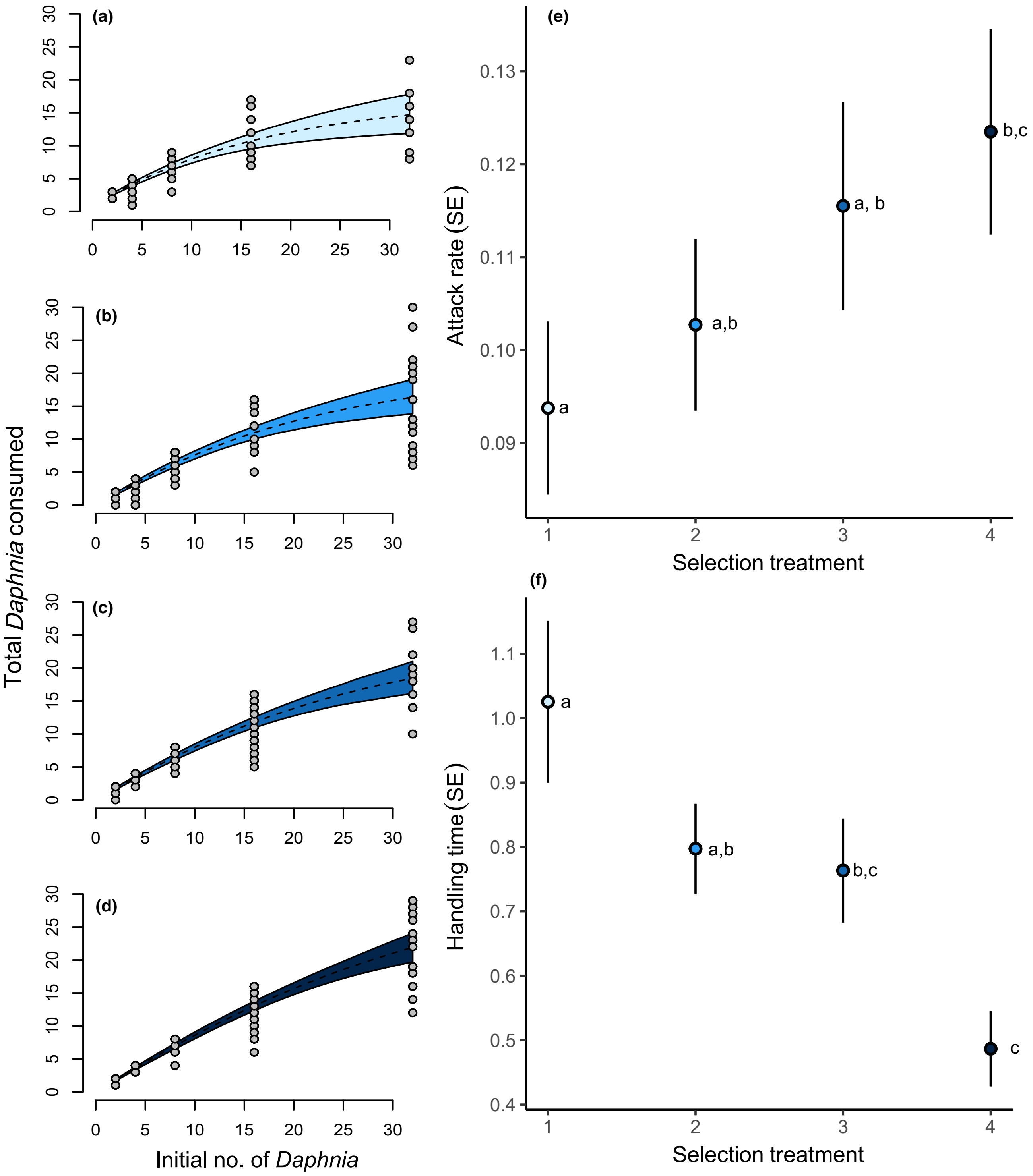

Figure 2 Effects of selection on activity altered damselfly functional responses to prey. (a–d) denote the functional response curves of damselflies from different selection levels; shaded coloured regions denote the 95% confidence intervals with colour coding as in Fig. 1. Small grey circles are individual damselflies. To illustrate, (a) shows strong selection for less active individuals to (d) showing strong selection for active individuals. (e) and (f) present the mean (±SE) attack rates and handling times respectively from each selection level; significant differences ($P < 0.05$) between pairwise comparisons are denoted by different letters.

DISCUSSION

That predators can influence prey population regulation and the strength of competition is taken as canonical (Gurevitch *et al.* 2000; Chase *et al.* 2002; Pringle *et al.* 2019). However, this body of work has mainly focused on either direct consumptive or immediate non-consumptive trait mediated effects, and not considered how selection mediates the

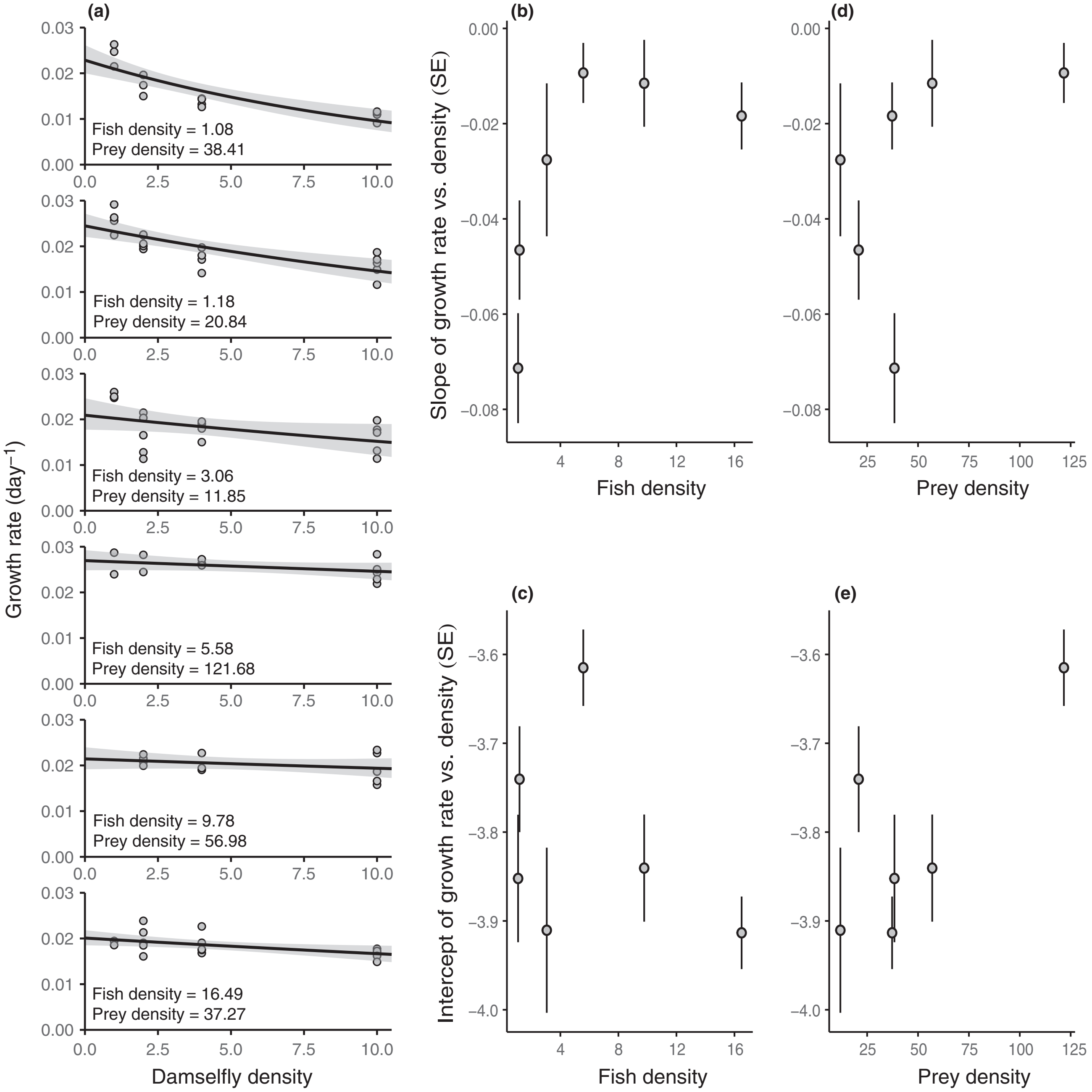

Figure 3 Strength of density dependence in damselfly growth rates declined with increasing fish density, but maximal growth rates increased with greater prey density. (a) Shows the relationship between damselfly growth rate and damselfly densities from field experiments replicated across lakes varying in fish densities and prey densities (inset values). Lines denote the log-linear regression and grey bands denote 95% CI. Panels in (a) are ordered by increasing fish densities from top to bottom. Model parameter estimates can be found in Table S2. (b) slopes and (c) intercepts from the log-linear models shown in (a) plotted in relation to fish density, and (d) slopes and (e) intercepts from the log-linear models in (a) plotted in relation to prey density.

feedback between these interactions. Our mesocosm experiment showed that selection on activity rates had cascading effects on the strength of intraspecific competition. In parallel, our field experiment found that the strength of competition was associated with the densities of predators, but not prey. Both experiments revealed that the strength of competition declined as selection for less active individuals increased. These results therefore support the hypothesised selection-driven coupling of predation and competition regulating prey populations and suggest that detecting this feedback might be obscured when only one of these components is considered.

This feedback does not require an evolutionary response to occur – selection can simply be an important within-generation ecological process. In fact, because heritability is rarely perfect, any ecological effects of adaptive evolution will reveal a muted effect of selection (Bailey *et al*. 2006). While strong eco-evolutionary dynamics can emerge when rapid evolutionary responses occur (Yoshida *et al*. 2003; Hendry 2016; McPeek 2017b), the ecological consequences of selection as a

Table 1 Results from the general linear model of damselfly growth rates in relation to damselfly density, fish density and prey density among lakes

Term	Estimate	SE	*t*	*P* value
Intercept	−3.854	0.059	−64.617	< 2e-16
Damselfly density	−0.059	0.01	−5.882	7.16e-08
Fish density	−0.009	0.005	−1.634	0.1058
Prey abundance	0.002	0.001	2.102	0.0384
Damselfly density × fish density	0.002	0.0009	2.454	0.0161
Damselfly density × prey density	0.0002	0.0002	1.68	0.0964

The overall model is significant ($F_{5,88} = 15.73$, $P = 4.839e\text{-}11$) with an $R^2 = 44.19$.

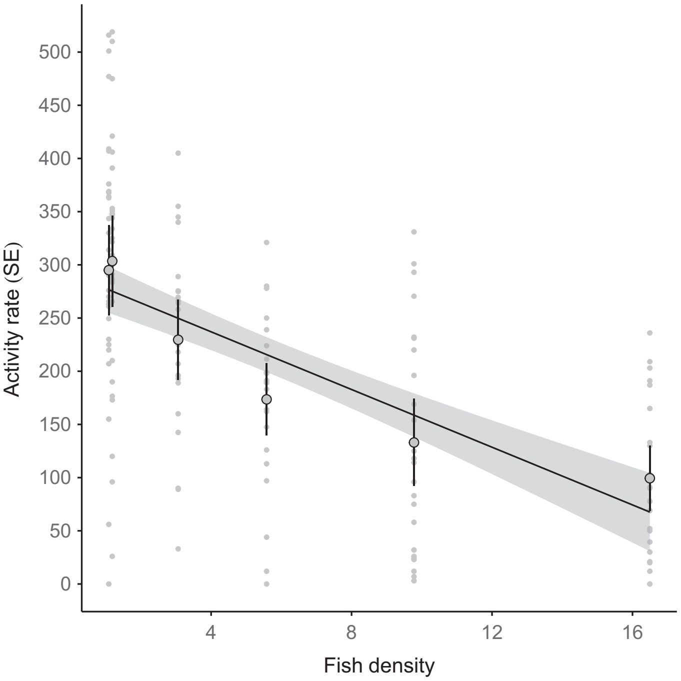

Figure 4 Damselfly activity rates declined with increasing fish densities. Shown is the linear regression (grey band denotes 95% CI) between activity rates (distance in mm moved per 3 h) in relation to estimated fish density. Large grey points denote the mean and error bars are the SE; small grey circles are individual damselfly activity rates. Model parameter estimates can be found in Table S3.

within-generation process that shapes intraspecific competition have been overlooked. Because intraspecific variation in traits mediating competitive ability and predation are frequently one and the same, and because intraspecific variation within and among populations in such traits is common (Stamps 2007), this feedback between ecological dynamics and evolutionary mechanisms may be pervasive in nature.

More generally, our findings illustrate the potentially elusive manner in which selection can modify the ecological dynamics of population regulation. The strong truncated selection generated in our mesocosm experiment is rare in nature, as it is unlikely that all mortality is selective and that threshold phenotypes exist (but see Urban 2007a). Indeed, although the mesocosm experiment provided proof of concept of the ecological impacts of selection, it also revealed a modest effect, accounting for < 10% of the variation in density dependence in growth rates. This is despite the fact that the selection imposed was quite strong relative to the typical strengths of selection in the wild (Kingsolver *et al.* 2001) or field experiments (Caruso *et al.* 2017). Thus, it may be that these effects are relatively weak in natural populations, varying with spatial and temporal differences in the strength of selection (Siepielski *et al.* 2009; Urban 2011).

The results of our mesocosm experiment showing the effect of selection altering attack rates and handling times, combined with extensions of consumer-resource models, such as the Rosenzweig & Macarthur (1963) model that couples trait and population dynamics through adaptive evolution (Abrams 2000; McPeek 2017a), would predict that increased damselfly attack rates or decreased handling times may cause equilibrium population sizes of damselflies to decline, even as fish densities decrease. That is, even when consumption by fish is relaxed, which should result in a larger damselfly population size, intraspecific competition would still strengthen to limit population growth because of shifts in activity rates and foraging ecology. Although we do not know equilibrium population sizes, our field experiment found that the strength of intraspecific competition increased as fish densities declined, which is consistent with this prediction. Because traits mediating growth (Shama *et al.* 2011) and activity (Swaegers *et al.* 2017) are heritable, the observed changes in density-dependent growth rates and activity levels among lakes reflect, in part, adaptive evolution. While fish cues were likely present, and plasticity may explain some of this variation (Siepielski *et al.* 2016a), our plasticity study showed that individual level differences were consistent in the presence or absence of fish predator cues (see also Start 2018).

A key implication of our findings therefore is that spatial variation in predator densities should differently affect the mechanisms regulating prey populations. At low fish densities, damselfly abundances are higher because predation from fish is lower (McPeek 1998; McPeek & Peckarsky 1998; Siepielski *et al.* 2010; Ousterhout *et al.* 2018). Under such conditions, damselflies experience relaxed selection from fish predation, which should maintain, if not favour, higher attack rates or reduced handling times since growth is food limited (McPeek 1998). Reduced predation therefore increases the strength of competition via both increased abundances and trait evolution, and competition likely becomes the dominant factor regulating populations. As a result, damselflies may locally adapt to be stronger competitors when predation is weak (Siepielski *et al.* 2016b). By contrast, damselfly mortality should be greater, and their abundances lower at high fish densities. Since predation becomes a stronger factor regulating damselfly populations, adaptive evolution to fish predation may prevent them from taking advantage of increased prey resources, or reduced aggressive encounters, which would occur at lower densities. For context, consider that ten-times more damselflies had a negligible effect on growth rates from lakes at high fish densities, but the same increase generated a precipitous decline in growth rates at low fish densities. This implies that the relative effects of competition and predation in regulating prey populations should vary spatially because of both consumption and selection. Thus, how organisms settle the growth-predation tradeoff varies with predator densities in a predictable fashion because of consumptive effects and phenotypic selection – providing a clue for how the growth-predation tradeoff may evolve.

While we do not know precisely which mechanism(s) explain how selection on activity mediates intraspecific competition, two seem likely. First, reduced activity would limit direct interference competition (Schoener 1983), since individuals would be less likely to encounter each other and engage in aggressive interactions (Start & Gilbert 2017). These aggressive interactions are not only costly because of injury that can arise during encounters, or the associated reductions in time spent foraging, but also because of strong stress responses that reduce growth (McPeek *et al*. 2001; Glennemeier & Denver 2002). Second, reductions in attack rates and increased handling times would diminish indirect exploitative competition for prey (McPeek 1998). Although we did not find that prey densities limited the strength of density dependence in growth rates among lakes, results from our field experiment support previous work indicating that growth rates are prey limited (McPeek 1998). Instead, density dependence in growth rates was more strongly associated with fish densities, which further implies that this density dependence may result more from interference competition generated through differences in activity. Additionally, we note that some variation in the strength of density dependence in damselfly growth rates could be explained by prey avoidance behaviour (Van de Meutter *et al*. 2004). If more prey moved out of the cages as damselfly density increased, this could reduce damselfly growth rates in a density-dependent fashion and intensify competition. Future work is needed to disentangle these possibilities and better understand the precise mechanism(s) generating variation in the strength of density dependence.

By considering the effects of selection imposed by predators on prey competitive dynamics, our results illustrate the pivotal role of intraspecific variation in food web dynamics (Bolnick *et al*. 2011; Gibert & DeLong 2017; Start & Gilbert 2017; Start 2018; Bolnick & Ballare 2020). Much like how non-consumptive trait-mediated effects can have consequences for community-level responses to predator-prey interactions (Peckarsky *et al*. 2008), these results likewise suggest that previous studies demonstrating density-dependent effects of predators on competition are not merely due to consumption, but may also capture the effects of selection. By examining how selection couples the direct (consumptive) and indirect (trait-mediated) effects of predators, we also gain a better understanding of the mechanisms that jointly influence predator-prey interactions and competitive dynamics of prey. From these efforts, we suggest it may be profitable to build a combined framework that establishes the effects of direct consumption, plastic trait mediated effects, ontogeny, selection and adaptive evolution (Govaert *et al*. 2016; Start 2018). Determining the combined contributions of such mechanisms is necessary for developing a comprehensive picture of the emergence of trait-mediated tradeoffs between predator-prey and competitive interactions embedded within food webs.

ACKNOWLEDGEMENTS

Comments from Sean Giery, Mark McPeek, Denon Start, and three anonymous reviewers on earlier versions of this ms greatly sharpened our thinking and presentation of this work. Wade Boys kindly helped with some of the experimental setup. We also thank the USFS and AGFC for facilitating access to field sites. This work was supported by funding from NSF (DEB 1748945) awarded to AMS.

AUTHORSHIP

AMS designed the study and wrote the first draft of the manuscript; AMS, AZK, TP, MS, KS and SPT gathered data; all authors revised the manuscript.

DATA AVAILABILITY STATEMENT

All data associated with this study are posted at Datadryad.org https://doi.org/10.5061/dryad.wdbrv15k2

REFERENCES

Abrams, P.A. (1984). Foraging time optimization and interactions in food webs. *Am. Nat*., 124, 80–96.

Abrams, P.A. (2000). The evolution of predator-prey interactions: theory and evidence. *Annu. Rev. Ecol. Syst*., 31, 79–105.

Anholt, B.R. (1990). An experimental separation of interference and exploitative competition in larval damselfly. *Ecology*, 71, 1483–1493.

Anholt, B.R. (1994). Cannibalism and early instar survival in a larval damselfly. *Oecologia*, 99, 60–65.

Bailey, J.K., Wooley, S.C., Lindroth, R.L. & Whitham, T.G. (2006). Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. *Ecol. Lett*., 9, 78–85.

Baker, R.L. (1981). Behavioural interactions and use of feeding areas by nymphs of *Coenagrion resolutum* (Coenagrionidae: Odonata). *Oecologia*, 49, 353–358.

Baker, R.L., Elkin, C.M. & Brennan, H.A. (1999). Aggressive interactions and risk of fish predation for larval damselflies. *J. Insect. Behav*., 12, 213–223.

Beckerman, A.P., Uriarte, M. & Schmitz, O.J. (1997). Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proc. Natl Acad. Sci. USA*, 94, 10735–10738.

Benkman, C.W. (2013). Biotic interaction strength and the intensity of selection. *Ecol. Lett*., 16, 1054–1060.

Bolnick, D.I. & Ballare, K.M. (2020). Resource diversity promotes among-individual diet variation, but not genomic diversity, in lake stickleback. *Ecol. Lett*., 23, 495–505.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M. *et al*. (2011). Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol*., 26, 183–192.

Bried, J.T. & Siepielski, A.M. (2019). Predator driven niches vary spatially among co-occurring damselfly species. *Evol. Ecol*., 33, 243–256.

Brodin, T. (2009). Behavioral syndrome over the boundaries of life—carryovers from larvae to adult damselfly. *Behav. Ecol*., 20, 30–37.

Brodin, T. & Johansson, F. (2004). Conflicting selection pressures on the growth/predation-risk trade-off in a damselfly. *Ecology*, 85, 2927–2932.

Caruso, C.M., Martin, R.A., Sletvold, N., Morrissey, M.B., Wade, M.J., Augustine, K.E. *et al*. (2017). What are the environmental determinants of phenotypic selection? A meta-analysis of experimental studies. *Am. Nat*., 190, 363–376.

Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D. *et al*. (2002). The interaction between predation and competition: a review and synthesis. *Ecol. Lett*., 5, 302–315.

Chesson, P. & Kuang, J.J. (2008). The interaction between predation and competition. *Nature*, 456, 235–238.

Endler, J.A. (1986). *Natural Selection in the Wild*. Princeton University Press, Princeton.

Gibert, J.P. & DeLong, J.P. (2017). Phenotypic variation explains food web structural patterns. *Proc. Natl Acad. Sci. USA*, 114, 11187–11192.

Glennemeier, K.A. & Denver, R.J. (2002). Role for corticoids in mediating the response of *Rana pipiens* tadpoles to intraspecific competition. *J. Exp. Zool.*, 292, 32–40.

Govaert, L., Pantel, J.H. & De Meester, L. (2016). Eco-evolutionary partitioning metrics: assessing the importance of ecological and evolutionary contributions to population and community change. *Ecol. Lett.*, 19, 839–853.

Gurevitch, J., Morrison, J.A. & Hedges, L.V. (2000). The interaction between competition and predation: a meta-analysis of field experiments. *Am. Nat.*, 155, 435–453.

Hammill, E., Atwood, T.B., Corvalan, P. & Srivastava, D.S. (2015). Behavioural responses to predation may explain shifts in community structure. *Freshw. Biol.*, 60, 125–135.

Hendry, A.P. (2016). *Eco-evolutionary dynamics*. Princeton University Press.

Johansson, F. (1993). Effects of prey type, prey density and predator presence on behaviour and predation risk in a larval damselfly. *Oikos*, 481–489.

Johansson, F. & Rowe, L. (1999). Life history and behavioral responses to time constraints in a damselfly. *Ecology*, 80, 1242–1252.

Johnson, D.M. (1991). Behavioral ecology of larval dragonflies and damselflies. *Trends Ecol. Evol.*, 6, 8–13.

Juliano, S., Scheiner, S. & Gurevitch, J. (2001). Design and analysis of ecological experiments. *Nonlinear curve fitting: predation and functional response curves*, 178–196.

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. *Am. Nat.*, 157, 245–261.

Kratina, P., Hammill, E. & Anholt, B.R. (2010). Stronger inducible defences enhance persistence of intraguild prey. *J. Anim. Ecol.*, 79, 993–999.

Lima, S.L. (1998). Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. In: *Advances in the Study of Behavior*. Elsevier, Amsterdam, Netherlands, pp. 215–290.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, 68, 619–640.

McNamara, J.M. & Houston, A.I. (1994). The effect of a change in foraging options on intake rate and predation rate. *Am. Nat.*, 144, 978–1000.

McPeek, M.A. (1990). Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. *Ecology*, 71, 83–98.

McPeek, M.A. (1998). The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecol. Monogr.*, 68, 1–23.

McPeek, M.A. (2000). Predisposed to adapt? Clade-level differences in characters affecting swimming performance in damselflies. *Evolution*, 54, 2072–2080.

McPeek, M.A. (2004). The growth/predation risk trade-off: so what is the mechanism? *Am. Nat.*, 163, E88–111.

McPeek, M.A. (2017a). The ecological dynamics of natural selection: traits and the coevolution of community structure. *Am. Nat.*, 189, E91–E117.

McPeek, M.A. (2017b). *Evolutionary Community Ecology*. Princeton University Press, Princeton, NJ.

McPeek, M.A. & Brown, J.M. (2000). Building a regional species pool: diversification of the *Enallagma* damselflies in eastern North America. *Ecology*, 81, 904–920.

McPeek, M.A. & Crowley, P.H. (1987). The effects of density and relative size on the aggressive behaviour, movement and feeding of damselfly larvae (Odonata: Coenagrionidae). *Anim. Behav.*, 35, 1051–1061.

McPeek, M.A. & Peckarsky, B.L. (1998). Life histories and the strengths of species interactions: combining mortality, growth, and fecundity effects. *Ecology*, 79, 867–879.

McPeek, M.A., Grace, J.M. & Richardson, J.M.L. (2001). Physiological and behavioral responses to predators shpae the growth/predation risk trade-off in damselflies. *Ecology*, 82, 1535–1545.

Ousterhout, B.H., Graham, S.R., Hasik, A.Z., Serrano, M. & Siepielski, A.M. (2018). Past selection impacts the strength of an aquatic trophic cascade. *Funct. Ecol.*, 32, 1554–1562.

Ousterhout, B.H., Serrano, M., Bried, J.T. & Siepielski, A.M. (2019). A framework for linking competitor ecological differences to coexistence. *J. Anim. Ecol.*, 88, 1534–1548

Paine, R.T. (1966). Food web complexity and species diversity. *Am. Nat.*, 100, 65–75.

Peacor, S.D. & Werner, E.E. (2001). The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Natl Acad. Sci. USA*, 98, 3904–3908.

Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, J.H., Luttbeg, B. *et al.* (2008). Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology*, 89, 2416–2425.

Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86, 501–509.

Pringle, R.M., Kartzinel, T.R., Palmer, T.M., Thurman, T.J., Fox-Dobbs, K., Xu, C.C. *et al.* (2019). Predator-induced collapse of niche structure and species coexistence. *Nature*, 570, 58.

Pritchard, D.W., Paterson, R., Bovy, H.C. & Barrios-O'Neill, D. (2017). Frair: an R package for fitting and comparing consumer functional responses. *Methods Ecol. Evol.*, 8, 1528–1534.

Rogers, D. (1972). Random search and insect population models. *J. Anim. Ecol.*, 41, 369–383.

Rosenzweig, M.L. & Macarthur, R.H. (1963). Graphical representation and stability conditions of predator-prey interactions. *Am. Nat.*, 97, 209–223.

Rueden, C.T., Schindelin, J., Hiner, M.C., DeZonia, B.E., Walter, A.E., Arena, E.T. et al. (2017). ImageJ2: ImageJ for the next generation of scientific image data. *BMC bioinformatics*, 18, 529.

Ruxton, G.D., Sherratt, T.N., Speed, M.P., Speed, M.P. & Speed, M. (2004). *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford University Press, Oxford, UK.

Schmitz, O.J., Krivan, V. & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.*, 7, 153–163.

Schoener, T.W. (1983). Field experiments on interspecific competition. *Am Nat*, 122, 240–285.

Shama, L.N.S., Campero-Paz, M., Wegner, K., De Block, M. & Stoks, R. (2011). Latitudinal and voltinism compensation shape thermal reaction norms for growth rate. *Mol. Ecol.*, 20, 2929–2941.

Siepielski, A.M., DiBattista, J.D. & Carlson, S.M. (2009). It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecol. Lett.*, 12, 1261–1276.

Siepielski, A.M., Hung, K.L., Bein, E.E.B. & McPeek, M.A. (2010). Experimental evidence for neutral community dynamics governing an insect assemblage. *Ecology*, 91, 847–857.

Siepielski, A.M., Fallon, E. & Boersma, K. (2016a). Predator olfactory cues generate a foraging–predation trade-off through prey apprehension. *Royal Soc. Open Sci.*, 3, 150537.

Siepielski, A.M., Nemirov, A., Cattivera, M. & Nickerson, A. (2016b). Experimental evidence for an eco-evolutionary coupling between local adaptation and intraspecific competition. *Am. Nat.*, 187, 447–456.

Sih, A. (1987). Predators and prey lifestyles: an evolutionary and ecological overview. Predation: Direct and Indirect Impacts on Aquatic Communities. *University Press of New England Hanover. A. Huhta et al. Sih, A. & Wooster, D. (1994) Prey behavior, prey dispersal and predator impacts on stream prey. Ecology*, 75, 1199–1207.

Sommers, P. & Chesson, P. (2019). Effects of predator avoidance behavior on the coexistence of competing prey. *Am. Nat.*, 193, E000–E000.

Stamps, J.A. (2007). Growth-mortality tradeoffs and 'personality traits' in animals. *Ecol. Lett.*, 10, 355–363.

Start, D. (2018). Ontogeny and consistent individual differences mediate trophic interactions. *Am. Nat.*, 192, 301–310.

Start, D. & Gilbert, B. (2017). Predator personality structures prey communities and trophic cascades. *Ecol. Lett.*, 20, 366–374.

Start, D., Kirk, D., Shea, D. & Gilbert, B. (2017). Cannibalism by damselflies increases with rising temperature. *Biol. Lett.*, 13, 20170175.

Steele, D.B., Siepielski, A.M. & McPeek, M.A. (2011). Sexual selection and temporal phenotypic variation in a damselfly population. *J. Evol. Biol.*, 24, 1517–1532.

Stoks, R. & De Block, M. (2000). The influence of predator species and prey age on the immediate survival value of antipredator behaviours in a damselfly. *Arch. Hydrobiol.*, 147, 417–430.

Strobbe, F., McPeek, M.A., De Block, M. & Stoks, R. (2011). Fish predation selects for reduced foraging activity. *Behav. Ecol. Sociobiol.*, 65, 241–247.

Swaegers, J., Strobbe, F., McPeek, M. & Stoks, R. (2017). Selection on escape performance during ecological speciation driven by predation. *Anim. Behav.*, 124, 153–159.

Travis, J., Leips, J. & Rodd, F.H. (2013). Evolution in population parameters: density-dependent selection or density-dependent fitness? *Am. Nat.*, 181, S9–S20.

Urban, M.C. (2007a). The growth–predation risk trade-off under a growing gape-limited predation threat. *Ecology*, 88, 2587–2597.

Urban, M.C. (2007b). Risky prey behavior evolves in risky habitats. *Proc. Natl Acad. Sci.*, 104, 14377–14382.

Urban, M.C. (2011). The evolution of species interactions across natural landscapes. *Ecol. Lett.*, 14, 723–732.

Van de Meutter, F., Stoks, R. & De Meester, L. (2004). Behavioral linkage of pelagic prey and littoral predators: microhabitat selection by Daphnia induced by damselfly larvae. *Oikos*, 107, 265–272.

Villalobos-Jiménez, G., Dunn, A.M. & Hassall, C. (2017). Environmental noise reduces predation rate in an aquatic invertebrate. *J. Insect Conserv.*, 21, 839–847.

Werner, E.E. & Anholt, B.R. (1993). Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am. Nat.*, 142, 242–272.

Werner, E.E. & Peacor, S.D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100.

Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. & Hairston, N.G. Jr (2003). Rapid evolution drives ecological dynamics in a predator–prey system. *Nature*, 424, 303.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Ian Donohue
Manuscript received 13 January 2020
First decision made 12 February 2020
Manuscript accepted 19 February 2020