

Research



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Eco-evolutionary feedbacks link prey adaptation to predator performance

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Eco-evolutionary feedbacks may determine the outcome of predator–prey interactions in nature, but little work has been done to quantify the feedback effect of short-term prey adaptation on predator performance. We tested the effects of prey availability and recent (less than 100 years) prey adaptation on the feeding and growth rate of largemouth bass (*Micropterus salmoides*), foraging on western mosquitofish (*Gambusia affinis*). Field surveys showed higher densities and larger average body sizes of mosquitofish in recently introduced populations without bass. Over a six-week mesocosm experiment, bass were presented with either a high or low availability of mosquitofish prey from recently established populations either naive or experienced with bass. Naive mosquitofish were larger, less cryptic and more vulnerable to bass predation compared to their experienced counterparts. Bass consumed more naive prey, grew more quickly with naive prey, and grew more quickly per unit biomass of naive prey consumed. The effect of mosquitofish history with the bass on bass growth was similar in magnitude to the effect of mosquitofish availability. In showing that recently derived predation-related prey phenotypes strongly affect predator performance, this study supports the presence of reciprocal predator–prey trait feedbacks in nature.

1. Introduction

Eco-evolutionary feedbacks—reciprocal interactions between ecological and evolutionary processes acting on similar timescales—are likely to shape the outcome of predator–prey interactions [1,2]. These feedbacks may be strong following the introduction of novel predators. After their introduction, predators can exhibit an initial period of exceptional performance because prey are abundant and naive [3–10]. This performance may quickly lapse as prey become depleted and as antipredator traits [7,11–14] and life-history adaptations (e.g. smaller size at maturation [15,16]) arise via plasticity and evolution. While changes in prey availability are known to have strong effects on predator performance, the feedback effect of changing prey traits on predator performance has rarely been examined, except in theory and chemostat experiments (e.g. [17–19]). Here, we experimentally disentangle the effects of availability and recent predation history of a prey species (mosquitofish, *Gambusia affinis*) for the performance of a predator species (largemouth bass, *Micropterus salmoides*).

Bass and mosquitofish strongly interact across their native range in the Southeastern USA and in their introduced ranges. Each species is economically valuable and has been introduced globally, including into California, USA (CA) [20]. Today in CA, mosquitofish occupy sites with bass as well as sites that lack predatory fishes. The length of their coexistence at specific sites in CA is not

known, but it must be recent, as mosquitofish were first introduced to CA in 1922 [21]. Where populations coexist, mosquitofish express traits that increase their survival in the presence of bass (i.e. adaptations), such as increased vigilance and streamlined body shapes that increase escape ability [22–24].

We first performed a field survey to test the prediction that mosquitofish populations with bass have smaller average body sizes (e.g. owing to decreased lifespan or earlier maturation) and lower abundances. Second, we used a mesocosm experiment to test how mosquitofish availability and recent predation history contribute to the predatory success of largemouth bass, and in turn bass growth. We expected bass performance to be reduced under low prey availability. We also expected bass performance to be reduced when feeding upon mosquitofish from populations with a recent history of predator exposure. This pattern would support the hypothesis that recent prey adaptation feeds back to affect predator performance, supporting the theory of reciprocal predator–prey eco-evolutionary feedbacks.

2. Material and methods

For the pond survey, we used standardized seine hauls to survey bass presence and mosquitofish density and size from 19 ponds in Santa Cruz, Mono, and Inyo Counties, CA (electronic supplementary material, table S1). Sites were chosen based on our knowledge of the distribution of mosquitofish in these counties. We found that 5 ponds had bass and 14 ponds did not have bass (electronic supplementary material, table S1). Some ponds with bass also had *Lepomis* spp., which less commonly prey upon mosquitofish [25].

We conducted a 2 × 2 factorial mesocosm experiment to determine the effects of mosquitofish availability (depletion or replacement treatments, see below) and population predation history (naive or experienced treatments) on bass prey consumption and growth rate. We established 32 mesocosms (1135 l, 65 cm depth, 170 cm diameter, Rubbermaid® USA) in a flat yard at the UCSC Coastal Science Campus (Santa Cruz, CA). We added equal amounts of sand and local pond sediment and zooplankton to each mesocosm (details in electronic supplementary material, figure S1). Mesocosms were left open for oviposition and colonization by macroinvertebrates. We installed one refuge (122 cm height, 30 cm diameter, 22 mm mesh) with artificial macrophytes per mesocosm where mosquitofish could avoid bass predation (electronic supplementary material, figure S1). We stocked a single one-year-old northern largemouth bass (*M. salmoides*, hatchery source: Freshwater Fish Co., Elk Grove, CA) per mesocosm. We measured the length and weight of bass before their introduction to mesocosms.

To test the effects of mosquitofish predation history, we stocked mosquitofish into mesocosms from a source pond either lacking bass ('naive' treatment, Northeast Spring) or with a high density of bass ('experienced' treatment, Furnace Creek Pond). We held mosquitofish in 100 l outdoor holding tanks (three per population) for 8 days on a diet of flake food before stocking. The focal sources had habitat and mosquitofish size traits representative of typical predator present and absent populations of mosquitofish (electronic supplementary material, table S1). The starting density of 10 mosquitofish per mesocosm (3.64 m⁻²) falls within the range of mosquitofish densities observed in natural ponds with bass (electronic supplementary material, table S1). We measured the length of all mosquitofish prior to their introduction to the mesocosms.

We crossed mosquitofish predation history with two mosquitofish availability treatments. A high-availability (replacement)

treatment was created by stocking 10 mosquitofish per mesocosm and maintaining that density throughout the experiment by replacing weekly any treatment fish consumed by bass. A low availability treatment (depletion) was created by introducing 10 mosquitofish but allowing bass predation to reduce mosquitofish density throughout the experiment, without replacement. To ensure no bass would starve, we hand-fed all bass two recently euthanized mosquitofish from a different site (Dodero Spring, Santa Cruz, CA) weekly throughout the experiment. Each of the four experimental treatments was replicated eight times, and treatments were assigned randomly across the mesocosm array.

We tracked mosquitofish abundance weekly in mesocosms; two to three observers counted the number of mosquitofish in mesocosms over separate 5-min observation periods. We used the maximum population count across observers to determine the number of replacement mosquitofish needed in replacement treatments. Replacement mosquitofish came from the same population used to establish that treatment. Replacement individuals were selected haphazardly from outdoor holding tanks kept adjacent to the mesocosm array. By comparing observer counts at the final timepoint with the actual number of fish recovered from the mesocosms, we corrected weekly survival (number surviving) for observer error (electronic supplementary material, figure S3). We then calculated the survival rate of mosquitofish for each mesocosm as the proportion of estimated surviving treatment fish from one week to the next, averaged over all weeks of the experiment.

We ended the experiment six weeks after fish introduction. We measured the length of all remaining mosquitofish. To estimate the total biomass of treatment mosquitofish added over the course of the experiment and the biomass of fish remaining, we used population-specific length–wet mass regressions generated from a large sample of fish at each site (electronic supplementary material, figure S2). To estimate mosquitofish biomass consumed, we took the difference in these values. We also measured the length and weight of the bass. We calculated the mean instantaneous growth rate *G* of bass from the individual's change in mass (g) over the duration of the experiment expressed in days [26]. Bass were frozen for preservation and then later dissected to obtain diet contents. Diet contents were removed from stomachs, identified and all invertebrates weighed.

For pond surveys, we compared the population density and mean body size of mosquitofish from naive versus experienced populations using Welch's *t*-tests. For the mesocosm experiment, we used a two-way ANOVA to test for effects of availability and history on our estimate of average mosquitofish survival, the biomass of mosquitofish consumed, the biomass of invertebrates in bass guts and log₁₀ bass growth. To test for pairwise differences among the four treatments, we used Tukey's HSD test. Interaction effects are reported below only when statistically significant (*p* < 0.05). We also calculated standardized effect sizes (Hedges' *g*) for each effect by response combination, on data as scaled (e.g. transformed or raw) for ANOVA tests (i.e. as shown in figure 1). We also tested whether history with predators affected the log₁₀ growth of bass per individual and per gram mosquitofish consumed. We conducted ANCOVAs with the number or biomass of mosquitofish consumed as a covariate, after confirming the homogeneity of slopes. We performed all analyses in R v. 3.4.1. [27]. Experimental data are available at Dryad [28].

3. Results

From the field survey, compared to ponds without bass, ponds with bass showed a 71% reduction in mosquitofish density (*t*_{17,0} = -2.67, *p* = 0.016), a 10% reduction in average

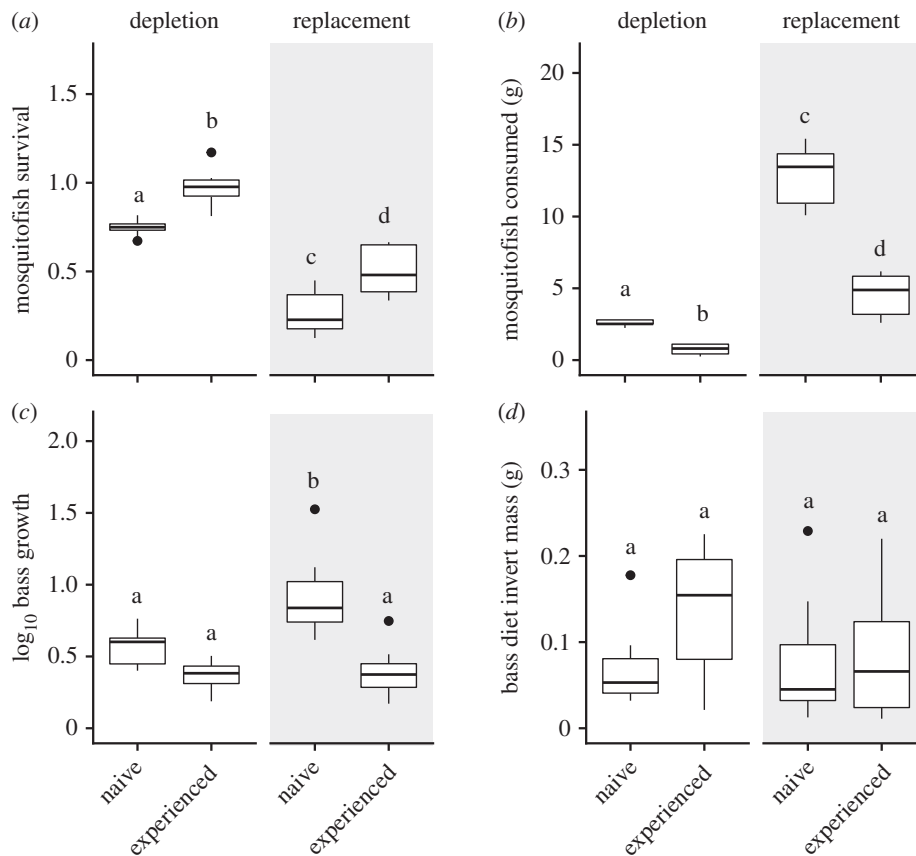


Figure 1. Responses by treatment of (a) estimated mosquitofish survival, as the average (across weeks) of the estimated proportion of mosquitofish surviving from week to week (i.e. 1 = 100% estimated average week to week survival, but values greater than 1 are possible owing to estimation errors; see electronic supplementary material, figure S5), (b) mosquitofish biomass consumed by bass over the course of the experiment, (c) mean instantaneous body growth rate G of bass over the course of the experiment and (d) the mass of invertebrate prey in bass diets at the end of the experiment. Letters represent homogenous subsets identified by *post hoc* tests (Tukey's HSD, 95%). The sample sizes are $n = 8$ mesocosms per treatment.

male length ($t_{14.9} = -4.29$, $p < 0.001$) and an 11% reduction in average female length ($t_{11.5} = -3.37$, $p = 0.006$) (electronic supplementary material, table S1). In the mesocosm experiment, mosquitofish from the experienced population were less readily detected by human observers, so we adjusted for this difference before calculating average weekly survival (electronic supplementary material, figure S3). Experienced mosquitofish exhibited higher average weekly survival than did mosquitofish from the naive population ($F_{1,28} = 16.8$, $p < 0.001$; figure 1a). Depletion treatments had higher average weekly survival than replacement treatments ($F_{1,28} = 75.2$, $p < 0.001$; figure 1a) because survival increased in depletion treatments through time (electronic supplementary material, figure S5). These trends in average weekly survival were consistent with trends in unadjusted overall survival over the course of the experiment (electronic supplementary material, figure S4). In mosquitofish depletion treatments, bass consumed fewer mosquitofish ($F_{1,28} = 245$, $p < 0.001$; figure 1b) and grew more slowly ($F_{1,28} = 7.54$, $p = 0.010$; figure 1c). In the presence of naive mosquitofish, bass consumed more mosquitofish ($F_{1,28} = 7.87$, $p = 0.009$; figure 1b) and grew faster ($F_{1,28} = 7.33$, $p = 0.011$; figure 1c). However, history and availability had an interactive effect on the biomass of mosquitofish consumed ($F_{1,28} = 48.2$, $p < 0.001$), as the effect of history was greater under mosquitofish replacement (figure 1b). We expected that reduced mosquitofish consumption might lead bass to switch to invertebrate food items, but we did not observe this effect ($p > 0.05$; figure 1d) and most

bass had few invertebrates in their guts. Standardized effect sizes (Hedges' g) showed that the effects of prey predation history were of similar strength to the effects of prey availability (figure 2a). Finally, ANCOVAs revealed that with naive prey, bass grew significantly more per individual mosquitofish consumed (figure 2b) and more per gram mosquitofish biomass consumed (figure 2c).

4. Discussion

We experimentally tested the effects of prey (mosquitofish) availability and recent prey predation history on the feeding and growth performance of a widely introduced predator (largemouth bass). As expected, bass consumed more mosquitofish and grew more under high mosquitofish availability. Bass consumed fewer mosquitofish and grew less in the presence of a mosquitofish population with a recent history of bass predation (figure 1). Interestingly, the strength of effects on bass performance due to mosquitofish availability was similar to the effects of mosquitofish predation history (figure 2a). Moreover, the relative decrease in bass growth with experienced mosquitofish was only partly owing to the lower biomass consumed (figure 2c), highlighting an important role for antipredator traits that increase the cost of foraging on experienced prey. Finally, because of the recent common ancestry among mosquitofish populations here (less than 100 years ago, roughly 250 generations), this

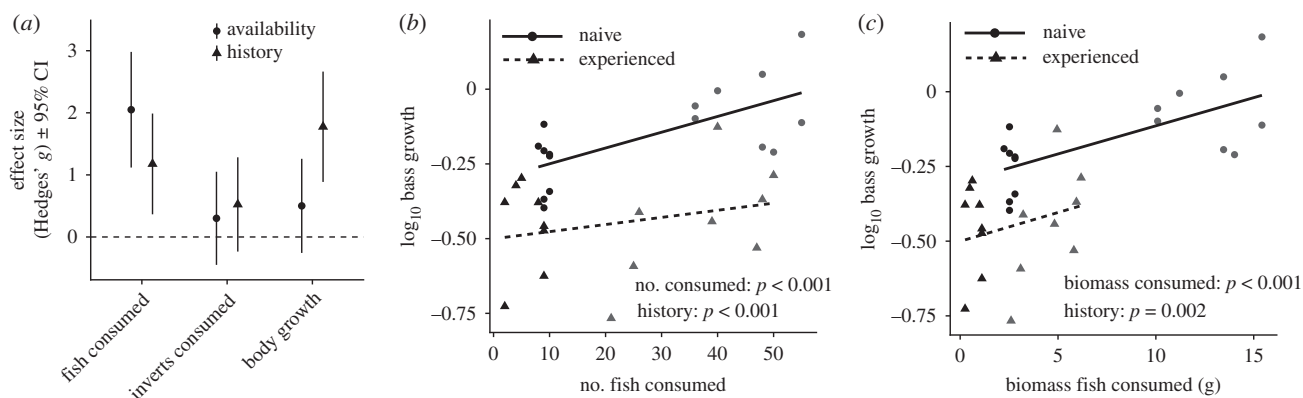


Figure 2. Standardized overall effect sizes (*a*; calculated from data shown in figure 1), and the effect of mosquitofish population predation history on the growth of bass (*b*) per individual mosquitofish consumed and (*c*) per gram mosquitofish consumed. (*b,c*) Black points represent depletion treatments and grey points represent replacement treatments.

study provides evidence that predator-induced prey trait changes feedback to reduce predator performance over short timescales, supporting reciprocal and ‘contemporary’ predator–prey trait feedbacks in nature.

In our pond surveys, mosquitofish populations without predators had higher densities and larger body size compared to populations from ponds with predators. In our experiment, bass consumed a significantly greater number and biomass of naive compared to experienced mosquitofish (figure 1*b*) and grew more quickly on naive prey. Bass grew more per naive mosquitofish consumed (figure 2*b*) in part because naive mosquitofish were larger in length (electronic supplementary material, table S1) and in weight at a given length (electronic supplementary material, figure S2). These prey size differences are likely to reflect more than simple demographic effects of shorter life expectancies (i.e. fewer older, larger individuals surviving). Together with earlier age at maturation, the smaller body size is a common adaptive response of prey to increased extrinsic mortality rates imposed by predators [15,16]. In addition, a thinner, more streamlined body is also known to be an adaptive response to predators in mosquitofish [23]. In our experiment, bass also grew more per gram biomass of naive mosquitofish consumed (figure 2*c*). This difference suggests a role for antipredator traits such as evasion and crypsis, which may have caused bass to be less efficient when preying upon experienced mosquitofish. Indeed, experienced mosquitofish populations showed increased survival (figure 1*a*; electronic supplementary material, figure S4) and decreased detection by human observers (electronic supplementary material, figure S3).

We used wild-caught fish in our experiment to capture the integrated phenotype associated with living with or without predators and arising from the effects of genetic adaptation and phenotypic plasticity. These traits and mechanisms ultimately act in concert to confer predator performance (dis)advantages. However, future work could expand our understanding by assessing the mechanisms associated with predator–prey trait feedbacks and their generality across evolutionary lineages. For example, reduced body size is a common response to predators, but reduced body size could confer antipredator advantages (e.g. crypsis) or disadvantages (e.g. decreased handling times [29]) independent of antipredator adaptation *per se*. Thus, it would be informative to experimentally parse the effects of reduced

prey body size from other prey traits associated with predation. Furthermore, the pace of changes to predator performance in nature will depend on the mechanisms of prey trait change. For example, the effects of prey learning will be rapid compared with the effects of prey evolution. Future work could aim to identify the underpinnings of prey trait changes (and their relative contributions) to understand the tempo of these predator–prey feedbacks. To do so, studies could use prey individuals and populations with varying lengths of predator exposure. The manipulation of exposure histories could also permit more relevant tests of the relative importance of prey traits versus prey availability. For example, in our experiment, the effect size of prey availability could have been unnaturally inflated, because we continually stocked individuals from containers without predator cues [30]. Finally, to assess the generality of the feedback effects reported here from our two focal prey populations, studies could check for parallel responses using multiple independent lineages of prey.

Overall, our data support theory and chemostat experiments that demonstrate the importance of predator–prey eco-evolutionary feedbacks [17–19]. Our results suggest that these effects operate in more complex ecosystems of management importance. From an invasive species perspective, these data suggest that invasive predator performance should lapse as antipredator traits arise in prey populations. More broadly, these data support a growing literature on ‘bottom-up’ eco-evolutionary effects, whereby changes in prey traits ‘feed up’ to affect predator ecology and traits [31,32]. Taken together with a relatively large literature on top-down eco-evolutionary effects [33], it may be that predation-related eco-evolutionary feedbacks are important and widespread in nature.

Ethics. The use of fish was approved by the CDFW (SC-12752) and the UCSC ethics board (Palke1506-2).

Data accessibility. Data have been uploaded to Dryad and the data are cited in the main text. Citation: Fryxell [28]. Experimental data from ‘Eco-evolutionary feedbacks link prey adaptation to predator performance’. Dryad Dataset (<https://doi.org/10.5061/dryad.0gb5mkkwn>). Readers can access the data via <https://datadryad.org/stash/share/RhHojbKirVHgj8S7xnfzdJETskrSCKAf1ArDyC-s9aQ>.

Authors’ contributions. D.C.F., E.P.P. and M.T.K. designed the study. R.R. led the field survey, with help from D.C.F. and E.P.P. D.C.F. and E.P.P. led the mesocosm experiment, with contributions from Z.T.W. and M.T.K. D.C.F. led analyses, with contributions from Z.T.W. and E.P.P. E.P.P. wrote the first draft of the introduction.

D.C.F. led writing thereafter, with contributions from Z.T.W., R.R., M.T.K. and E.P.P. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests

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