



# Prey adaptation along a competition-defense tradeoff cryptically shifts trophic cascades from density- to trait-mediated

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## Abstract

Trophic cascades have become a dominant paradigm in ecology, yet considerable debate remains about the relative strength of density- (consumptive) and trait-mediated (non-consumptive) effects in trophic cascades. This debate may, in part, be resolved by considering prey experience, which shapes prey traits (through genetic and plastic change) and influences prey survival (and therefore density). Here, we investigate the cascading role of prey experience through the addition of mosquitofish (*Gambusia affinis*) from predator-experienced or predator-naïve sources to mesocosms containing piscivorous largemouth bass (*Micropterus salmoides*), zooplankton, and phytoplankton. These two sources were positioned along a competition-defense tradeoff. Results show that predator-naïve mosquitofish suffered higher depredation rates, which drove a density-mediated cascade, whereas predator-experienced mosquitofish exhibited higher survival but fed less, which drove a trait-mediated cascade. Both cascades were similar in strength, leading to indistinguishable top-down effects on lower trophic levels. Therefore, the accumulation of prey experience with predators can cryptically shift cascade mechanisms from density- to trait-mediated.

**Keywords** Predator experience · Trophic cascades · Consumptive effects · Non-consumptive effects · Competition-defense tradeoffs · Cryptic dynamics · *Gambusia affinis*

## Introduction

Trophic cascades—effects of predators that propagate downward through food webs (Paine 1980; Ripple et al. 2016)—are a dominant but frequently-revisited (Strong 1992; Polis et al. 2000; Shurin et al. 2002; Borer et al. 2005) paradigm in ecology. Understanding the mechanisms underlying trophic

cascades is essential to understanding how manipulation of one trophic level will affect entire food webs (Finke and Denno 2004; Fahimipour et al. 2017). Trophic cascades are of broad environmental concern since the addition of novel predators (e.g. invasive species) (Walsh et al. 2016) or removal of top-predators (e.g. harvest) (Frank et al. 2005; Daskalov et al. 2007) can reshape entire food webs.

Trophic cascades can be driven by *consumptive*—or *density-mediated*—effects, in which changes in prey abundance propagate through food webs, and *non-consumptive*—or *trait-mediated*—effects, in which changes in prey functional traits (often behavior) propagate (Schmitz et al. 1997; Grabowski and Kimbro 2005; Preisser and Bolnick 2008a). There has been persistent debate in the literature over which mechanism is stronger or more common, with little practical consensus (Peacor and Werner 2001; Křivan and Schmitz 2004; Schmitz et al. 2004; Trussell et al. 2006; Preisser and Bolnick 2008b; Peacor et al. 2013). However, density- and trait-mediated interactions are likely inter-dependent, as prey traits that generate trait-mediated trophic cascades (e.g. predator avoidance) also increase survival (Sih et al. 2010). Thus, interacting density- and trait-mediated

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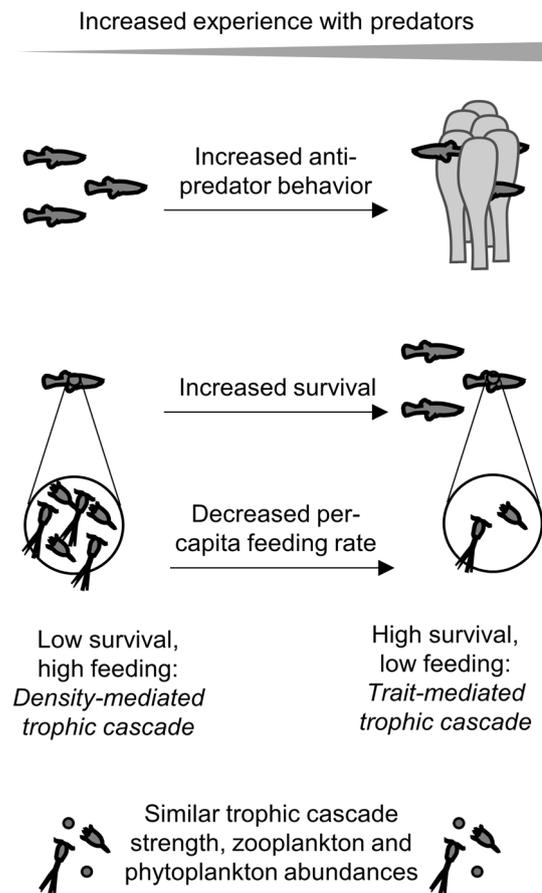
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processes should be considered together to assess the nature and strength of trophic cascades and maximize predictive power (Griffiths et al. 2018). Our work aims to elucidate the role of prey experience with predators in shaping whether density- or trait-mediated processes will dominate.

Prior experience with predators can mediate the extent to which predator introductions cause density and trait changes in prey populations. Through phenotypic plasticity (McCormick and Holmes 2006; Lönnstedt et al. 2012), trans-generational plasticity (e.g. epigenetic and maternal effects) (Storm and Lima 2010), and genetic evolution (Wund et al. 2015), accrued experience with predators can lead prey populations to display antipredator behaviors that enhance survival. Experience with native predators may also increase prey survival rates in the face of a novel predator (Dunlop-Hayden and Rehage 2011). Antipredator behaviors that increase prey survival include fleeing (Langerhans 2009), aggregating (Seghers 1974; Magurran et al. 1992), freezing (Vilhunen and Hirvonen 2003; Eilam 2005), hiding (Romare and Hansson 2003; Templeton and Shriner 2004), and predator inspection (Magurran 1986; Magurran et al. 1992). Such behaviors may lead to a decrease in feeding in a given habitat if they restrict the space or time available for foraging (Schmitz et al. 2004). Thus, natural selection imposed by predators may shift populations along a feeding-survival tradeoff where individuals from predator-experienced populations survive longer but feed less in the face of predators. Indeed, such tradeoffs have been demonstrated across suites of species, following predictable bold and fast versus slow and shy trait patterns (Stearns 1989; Johnson 1991). This adaptive tradeoff could shape the strength of trait- and density-mediated processes (Peacor et al. 2013). Furthermore, adaptation along this tradeoff can generate cascading ecological effects by modifying feeding behavior, morphology, and prey capture success (Bassar et al. 2010; Palkovacs et al. 2011; Ingram et al. 2012; Ousterhout et al. 2018; Wood et al. 2018; Start 2018).

We hypothesized that prior prey experience with predators dictates the extent to which trophic cascades induced by predators are density- or trait-mediated (Fig. 1). Naïve prey are less likely to exhibit antipredator behaviors, and thus may suffer high mortality upon predator introduction, driving a density-mediated trophic cascade. Experienced prey are more likely to employ antipredator behaviors, which decrease mortality rates (Sih et al. 2010). However, reduced feeding in risky habitats should alternatively generate a trait-mediated trophic cascade (Trussell et al. 2006). In theory, the form of this competition-defense tradeoff should dictate the relative strength of interacting density- versus trait-mediated trophic cascades.

Here we investigate the cascading ecological consequences of prior prey experience with predators for western mosquitofish (*Gambusia affinis*) exposed to piscivorous



**Fig. 1** Anti-predator experience, which is driven by genetic and plastic adaptation, may shape the strength of density- and trait-mediated trophic cascades. Predator-naïve prey are predicted to have high feeding and high mortality rates, leading to a density-mediated trophic cascade. Predator-experienced prey are predicted to have low feeding and low mortality rates, driving a trait-mediated trophic cascade

largemouth bass (*Micropterus salmoides*). Mosquitofish are an ideal study system to address the cascading effects of prey experience because they have strong effects on pelagic communities (Hurlbert et al. 1972; Hurlbert and Mulla 1981; Pyke 2008) and established capacity for antipredator adaptation (Langerhans et al. 2004; Langerhans and Makowicz 2009; Wood et al. 2019; Fryxell et al. 2019). We established pond mesocosms seeded with phytoplankton and zooplankton, then added bass and predator-experienced or predator-naïve source mosquitofish. These two populations typified an experience-driven competition-defense tradeoff, with the experienced population having higher survival but poorer feeding success. Such tradeoffs are a common feature of antipredator adaptation and have the potential to drive adaptive ecological dynamics (Abrams and Matsuda 1997; Yoshida et al. 2004; Hiltunen et al. 2014; Kasada et al. 2014; Wood et al. 2018).

We quantified cascading effects of bass predators as contingent on mosquitofish experience, separating density-mediated (survival) and trait-mediated (per-capita consumption) effects. Mosquitofish introduction in similar mesocosm experiments has repeatedly revealed clear trophic cascades, with most zooplankton abundances decreasing and phytoplankton increasing as a result (Hurlbert et al. 1972; Fryxell et al. 2015, 2016; Fryxell and Palkovacs 2017). Therefore, we expected bass introduction to generally cause the opposite response, decreasing mosquitofish abundances, increasing zooplankton, and decreasing phytoplankton. However, we expected the dominant cascade mechanism (density or traits) to depend on prior exposure of mosquitofish to largemouth bass, with naïve mosquitofish causing a density-mediated cascade and experienced mosquitofish showing a trait-mediated cascade.

## Methods

### Fish sources

We collected mosquitofish using hand nets and beach seines from two ponds in eastern California in March 2016:

(1) Fish Slough Northeast Spring (N 37.518003°, W 118.400157°), which is protected from downstream predators (United States Bureau of Land Management and U.S. Fish and Wildlife Service 1985) by a dam and diligent predator monitoring and removal for at least the past 30 years (US Fish and Wildlife Service 2005), and

(2) Furnace Creek Pond (N 36.460453°, W 116.872978°), which contains a high density of largemouth bass (*Micropeters salmoides*) since at least 2012 (but probably much earlier, DCF, personal observation) and no other piscine mosquitofish predators.

Both of these ponds are small, clearwater, spring-fed desert ponds. Largemouth bass are a common mosquitofish predator and play a strong role in mosquitofish functional ecology (Langerhans et al. 2004; Langerhans 2009; Wood et al. 2019). We classified mosquitofish from these ponds as predator-naïve and predator-experienced, respectively. These populations together represent clear endpoints of mosquitofish antipredator experience, as predators are diligently removed from the predator-naïve source (United States Bureau of Land Management and U.S. Fish and Wildlife Service 1985; US Fish and Wildlife Service 2005), and predation is so heavy at the predator-experienced source that mosquitofish startled out of hiding by the authors were immediately consumed by bass waiting nearby. We confirmed in this study that these populations exhibited typical patterns of a competition-defense tradeoff, with the predator-experienced population showing higher survival rates but lower feeding rates around bass than the predator-naïve

population (see below). Thus, this study is an analysis of cascading impacts of prey adaptation at endpoints of a potential competition-defense tradeoff, not a census of the ecological impacts of various mosquitofish populations. Furthermore, mosquitofish density and body size in these populations are consistent with other experienced and naïve populations (Table S-1). Because we were concerned with the maximum functional (ecological) scope of mosquitofish antipredator experience (plastic and genetic), we used fish collected from the wild in this experiment. Prey experience thus represents combined influences of genetic evolution, maternal effects, and phenotypic plasticity. We held fish in 100 L tanks (3 tanks per population) for 8 days on a diet of TetraMin tropical flakes before they were stocked into experimental mesocosms.

### Mesocosm experiment

Our experiment used 32 mesocosms in Santa Cruz, California in March 2016. We filled each 1,100 L mesocosm (1.75 m wide, 0.64 m high) with municipal water and 18.5 L of sand, then added 4 L of homogenized sediment from two nearby ponds: West Lake (N 36.976083°, W 122.045683°) and Antonelli Pond (N 36.955566°, W 122.060489°). We also added homogenized zooplankton from the above ponds. We installed plastic mesh cylinders (29 cm diameter, 22 mm mesh) filled with plastic artificial macrophytes as mosquitofish refuges from predation (mosquitofish could enter the refuge and used it freely; bass were excluded by the mesh). We allowed mesocosms to equilibrate for 15 days prior to fish introductions. We introduced 10 predator-experienced or predator-naïve mosquitofish into each experimental mesocosm (16 mesocosms per fish source). This density of mosquitofish ( $3.64 \text{ m}^{-2}$ ) is within the range of mosquitofish densities observed in the wild from ponds with largemouth bass (Table S-1). We introduced a single one-year-old bass (mean length  $\pm$  standard deviation =  $11.9 \pm 1.0$  cm) from a hatchery source (Freshwater Fish Co., Elk Grove CA) into half of the mesocosms for each mosquitofish treatment. We used the bass-present mesocosms to detect the role of mosquitofish experience in mediating cascades caused by bass; we used the bass-absent mesocosms to confirm the presence of a bass-driven trophic cascade.

To measure the effects of largemouth bass on mosquitofish density, we conducted weekly visual counts of the mosquitofish in each mesocosm. An observer standing adjacent to each mesocosm counted all mosquitofish seen during a 5-minute interval. A second observer repeated this process for an additional 5-minute interval. If the mosquitofish counts differed between observation periods, a third observer did an additional 5-minute observation. At the end of the experiment, we used paired visual counts (using the methods above) and exhaustive netting of all mosquitofish in each

mesocosms to build an observed ~ actual mosquitofish count relationship (see Supplemental Methods, Figure S-1, Table S-2). We used this relationship to correct our mosquitofish counts from earlier in the experiment; these corrected counts were used for all successive analyses. Decreases in mosquitofish density in the bass-present mesocosms were presumed to be due to predation by bass, as there was no mosquitofish mortality in the bass-absent mesocosms, and we observed no mosquitofish remains in the bass-present mesocosms.

We sampled zooplankton and phytoplankton weekly for 6 weeks after fish introduction. Zooplankton were collected from 1 L depth-integrated water samples, preserved in 80% ethanol, and identified under a dissecting microscope. Phytoplankton concentrations were measured using pelagic chlorophyll-*a* (chl-*a*), collected using 1 L depth integrated water samples, filtered onto 0.7 µm filters (Whatman GF/F), and measured using fluorometry (Turner Designs, Trilogy Module CHL-NA). We estimated 24-h gross primary production (GPP) using diel changes in dissolved oxygen concentrations (Harmon et al. 2009).

## Analyses

We conducted all analyses in this study in R (R Core Team 2016).

### Bass-induced trophic cascades

We fit the following general linear model to examine the cascading effect of bass presence and mosquitofish experience on consumers (zooplankton) and producers (phytoplankton) in all mesocosms:

$$N = \beta_0 + \beta_1 \times B + \beta_2 \times S_{\text{bass present}} + \beta_3 \times S_{\text{bass absent}} + \beta_4 \times W + \beta_5 \times W^2 + \beta_6 \times B \times W + \beta_7 \times S_{\text{bass present}} \times W + \beta_8 \times S_{\text{bass absent}} \times W + \beta_9 \times B \times W^2 + \beta_{10} \times S_{\text{bass present}} \times W^2 + \beta_{11} \times S_{\text{bass absent}} \times W^2, \quad (1)$$

where  $N$  is the concentration or density of each response variable,  $\beta$  terms are coefficients determined during model-fitting,  $B$  is bass presence,  $S_{\text{bass present}}$  and  $S_{\text{bass absent}}$  are mosquitofish source nested within bass presence or absence, respectively, and  $W$  is week (numeric).

This model allows us to analyze the ecological consequences of mosquitofish experience within the context of bass presence, i.e. separately for bass present vs. bass absent mesocosms. This model produces the same predictive result as a factorial model that crosses mosquitofish experience  $\times$  bass presence (by producing a unique intercept and slope for each mosquitofish experience  $\times$  bass presence combination), but with the added benefit of allowing us to

statistically test for ecological effects of mosquitofish experience separately in bass present vs. absent contexts. This design is akin to establishing linear contrasts in an analysis of variance. We treat week ( $W$ ) as continuous linear and quadratic fixed variables here as we are also interested in how bass presence and mosquitofish experience influence the development of trophic cascades over time. We included quadratic terms due to obvious curvilinear patterns in the data (see “Results”). We used type II likelihood ratio tests to examine the statistical significance of each term in the model.

### Mosquitofish survival

We analyzed weekly mosquitofish survival rate using a general linear model of the following form:

$$F_{t+1} = F_t \times L_S, \quad (2)$$

where  $F$  is number of mosquitofish,  $t$  is time (in weeks), and  $L_S$  is a source-specific coefficient. We used a likelihood ratio test to determine whether  $L_S$  varied significantly across predator-experienced and predator-naïve sources.

### Per-capita cascading effects of mosquitofish experience

Due to the significant effect of mosquitofish experience on zooplankton composition only when bass were absent (see “Results”), we dug deeper into the feeding and survival trends of the two mosquitofish sources in the presence of bass. We analyzed per-capita effects of mosquitofish on consumers (zooplankton) and producers (phytoplankton) within the bass-present mesocosms using a two-step general linear mixed model. The first step predicted responses based solely on a random time effect. The second step predicted the residuals from the first step with a fixed, source-specific fish abundance effect and a random mesocosm identity effect. Removing time effects before considering fish abundance effects avoided conflating successional changes in mesocosm communities with top-down effects of mosquitofish abundance. Our model formulations were as following:

$$N = \beta_0 + T + \varepsilon_0, \quad (3a)$$

$$\varepsilon_0 = \beta_1 + F^{1/3} \times C_S + M + \varepsilon_1, \quad (3b)$$

where  $N$  is the concentration or density of each response variable,  $\beta_0$  and  $\beta_1$  are intercepts,  $T$  is a random (categorical) time effect,  $\varepsilon_0$  and  $\varepsilon_1$  are residuals,  $F$  is number of mosquitofish (calculated as the average of fish observed at the beginning and end of each week),  $C_S$  is a source-specific coefficient, and  $M$  is a random mesocosm identity effect. We  $\ln(X+1)$  transformed zooplankton abundances for normality. We included the effect of mosquitofish as a

nonlinear term due to obvious non-linear trends in the data (see "Results", Table S-3). We included all time points for this analysis (i.e. mosquitofish survival data from weeks 1–6 and ecological data from weeks 2–6—due to the way  $F$  was calculated). We used maximum-likelihood (non-restricted) model fitting within the *lme4* package in R for all mixed models (Bates et al. 2015). See Table S-4 for full model parameter estimates.

For each response variable, we used likelihood ratio tests to sequentially test for effects of mosquitofish density, then source-specific effects of mosquitofish density. Significant source-specific effects of mosquitofish density indicated that mosquitofish from the different sources had different per-capita consumptive or cascading effects on zooplankton or producers, respectively. We analyzed the following broad taxonomic groups for zooplankton: all adult crustaceans, copepods (together or separated into adults, copepodites, and nauplii), cladocerans (together, or separated into *Bosmina*, *Daphnia*, and *Ceriodaphnia*), and rotifers. Mosquitofish consume all of the above taxa (Mansfield and Mcardle 1998) and commonly reduce their abundances upon introduction (Hurlbert and Mulla 1981).

## Results

Here bass introduction resulted in large increases in zooplankton abundance (Fig. 2, Table 1, Table S-5). However, while predator-experienced mosquitofish had higher survival around bass (Fig. 3), there were no differences in bass-induced trophic cascade strength due to mosquitofish source (Fig. 2, Table 1). Analysis of per-capita impacts of the two mosquitofish sources on zooplankton indicate that the greater survival of predator-experienced mosquitofish is offset by a lower feeding rate (Figs. 4, 5).

### Bass-induced trophic cascades

Our mesocosms showed a clear bass-mosquitofish-zooplankton trophic cascade, such that zooplankton were more abundant in mesocosms with bass (Fig. 2, Table 1). Furthermore, we documented negative interactions between bass and mosquitofish (Fig. 3), and between mosquitofish and zooplankton (Fig. 4), indicating a clear pathway for a top-down trophic cascade. Interestingly, while predator experience in mosquitofish led to decreased zooplankton densities when bass were absent (Fig. 2, Table 1), there were no effects of mosquitofish source on trophic cascade strength when bass were present (Fig. 2, Table 1).

### Mosquitofish survival

Predator-experienced mosquitofish had significantly higher weekly survival rates compared to predator-naïve mosquitofish ( $0.86 \pm 0.04$  vs.  $0.52 \pm 0.09$ , respectively;  $\chi^2 = 11.4$ ,  $df = 1$ ,  $p < 0.001$ ; Fig. 3). This survival difference led predator-experienced mosquitofish to persist much longer in mesocosms than predator-naïve mosquitofish (Fig. 3).

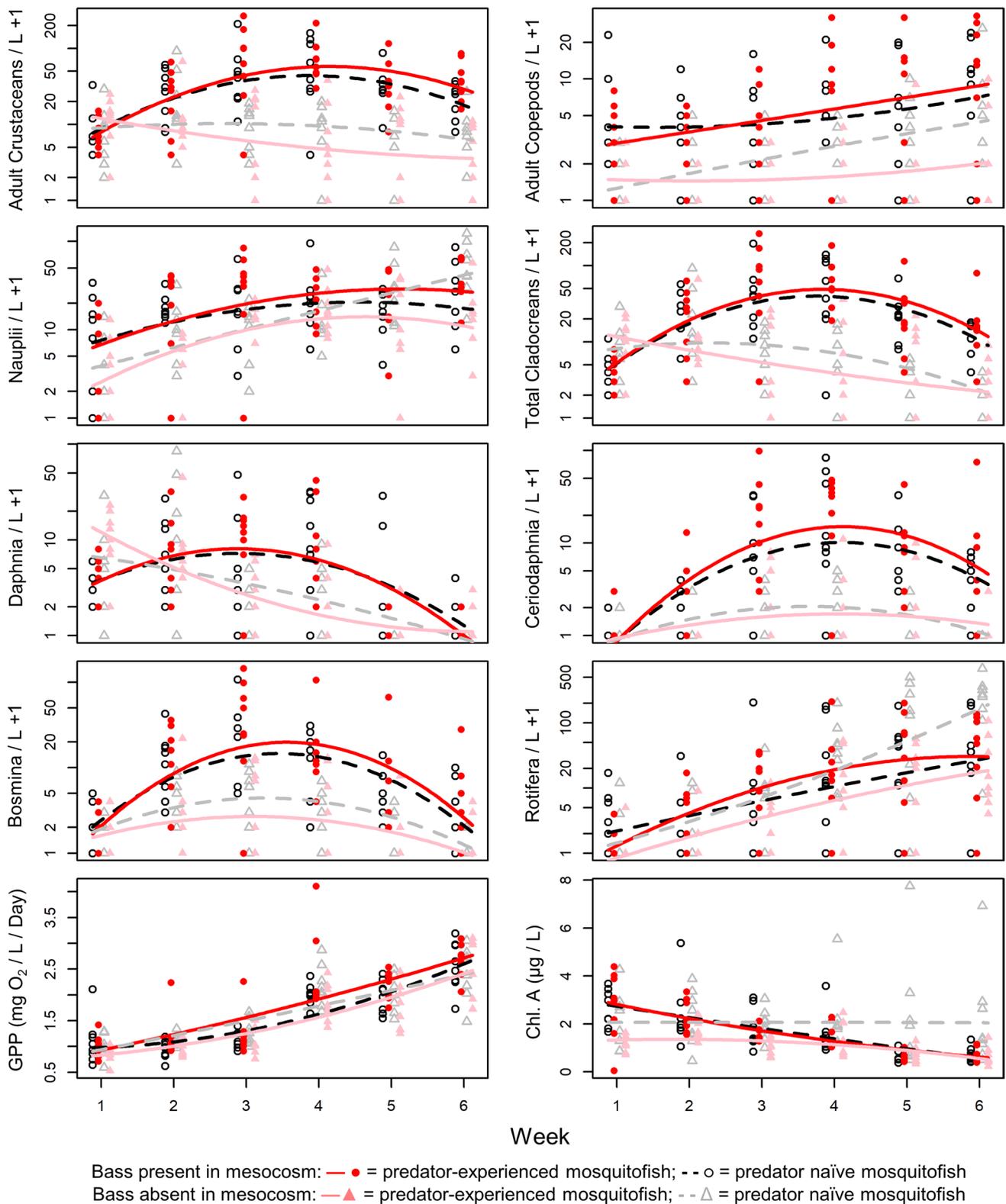
### Per-capita cascading effects of mosquitofish experience

Despite the much higher survival rate of predator-experienced mosquitofish (Fig. 3), there were no major differences in any observed zooplankton or producer abundances across mosquitofish treatments within the bass-present mesocosms (Fig. 2, Table 1). When bass were present, predator-naïve mosquitofish had stronger estimated per-capita consumptive effects on adult crustaceans, nauplii, rotifers, than predator-experienced mosquitofish (Fig. 4, Table 2). Combining the estimated source-specific effects of mosquitofish on zooplankton (above) and survival rates revealed a feeding-survival tradeoff, in which the predator-naïve population had higher apparent zooplankton consumption rates but lower survival rate (Fig. 5).

## Discussion

Our results show that prey experience with predators, likely resulting from a mixture of adaptation and plasticity (Arnett and Kinnison 2017), determined the extent to which mosquitofish density versus traits mediated the strength of the bass-mosquitofish-zooplankton trophic cascade. Predator-naïve mosquitofish had lower survival in the presence of bass but higher per-capita feeding rates, whereas predator-experienced mosquitofish had higher survival and lower per-capita feeding rates. Thus, the high mortality of predator-naïve mosquitofish facilitated a stronger density-mediated trophic cascade, whereas the low feeding rate of predator-experienced mosquitofish facilitated a stronger trait-mediated trophic cascade (Fig. 1). Importantly, the competition-defense tradeoff exhibited across mosquitofish sources when bass were present (Fig. 5) mediated net trophic cascades of roughly equal strength. In other words, there was no significant difference in zooplankton abundances between the two treatments despite the predator-naïve treatment having significantly lower mosquitofish density following bass addition. Prior prey experience with predators cryptically shifted the dominant trophic cascade mechanism from density-mediated to trait-mediated.

Prey experience with predators, via plasticity and heritable adaptation, can thus mediate the cascading effects



**Fig. 2** Bass induced a trophic cascade that increased abundances of nearly all zooplankton, and this trophic cascade was strongest at intermediate time-scales. Bass-experienced mosquitofish (*Gambusia affinis*) led to decreased abundances of some zooplankton and chlorophyll a, but only when bass were absent. When bass were present,

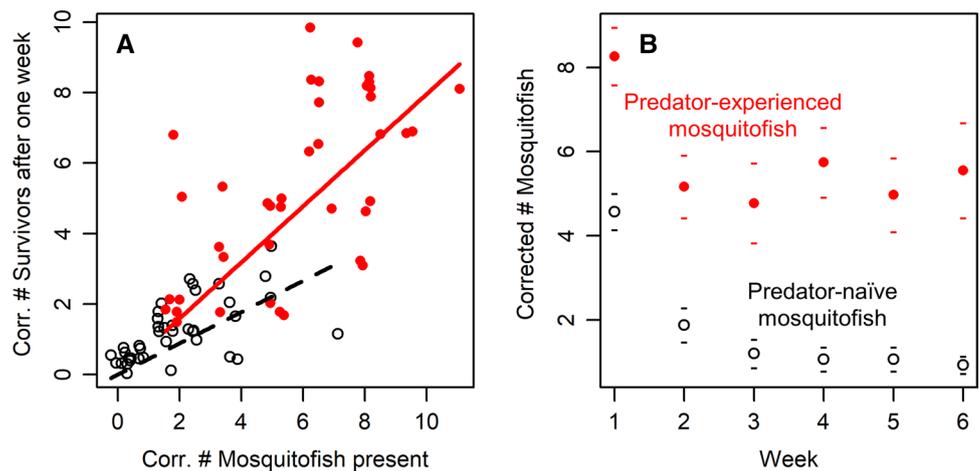
mosquitofish experience with bass led to no discernable differences in any measured ecological trait. Each point within each time represents a unique mesocosm. Lines indicate predictions from a general linear model (Eq. 1)

**Table 1** Bass induced a trophic cascade that increased abundances of nearly all zooplankton, and this trophic cascade was strongest at intermediate time-scales

Abundance or metric	Bass	Mosquitofish experience, bass present	Mosquitofish experience, bass absent	Week, week <sup>2</sup>	Bass × week, week <sup>2</sup>	Mosquitofish experience, bass present × week, week <sup>2</sup>	Mosquitofish experience, bass absent × week, week <sup>2</sup>
Adult crustaceans	+		-	∩	∩		
Adult copepods	+		-				
Nauplii	+		-	∩			
Cladocerans	+		-	∩	∩		
Daphnia	+		-	∩	∩		
Ceriodaphnia	+		-	∩	∩		
Bosmina	+		-	∩	∩		
Rotifers			-	+			
GPP							
Chlorophyll <i>a</i>			-				

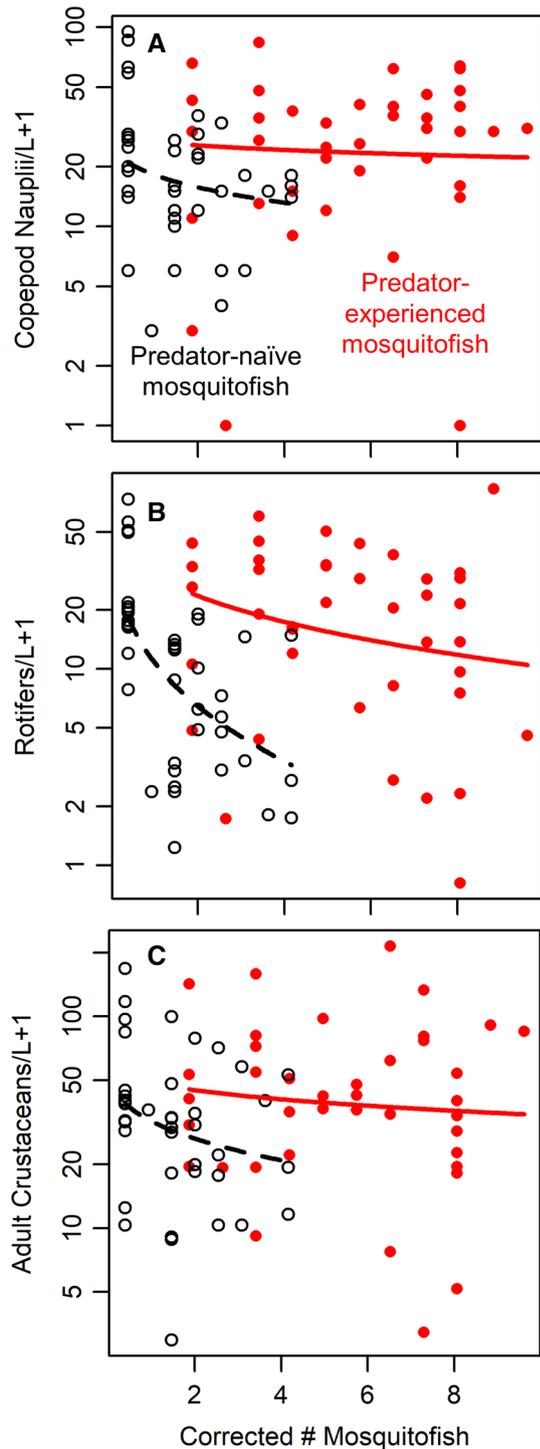
Bass-experienced mosquitofish led to decreased abundances of some zooplankton and chlorophyll *a*, but only when bass were absent. When bass were present, mosquitofish experience with bass (source) led to no discernable differences in any measured ecological trait. + indicates a positive impact on the ecological trait, ∩ indicates a negative impact, ∩ indicates a quadratic relationship. For significance tests, see Table S-5. *N* = 192

**Fig. 3** Mosquitofish from a predator-experienced source had higher week-to-week survival rates than mosquitofish from a predator-naïve source (a) and thus persisted longer in mesocosms with bass (b). Data from weeks 1–6 are pooled for a, and points are jittered to aid visual comprehension. Lines on a show general linear model predictions for each source-type. Bars on b show ± one standard error. *N* = 80 for (a) and 8 per point for (b)

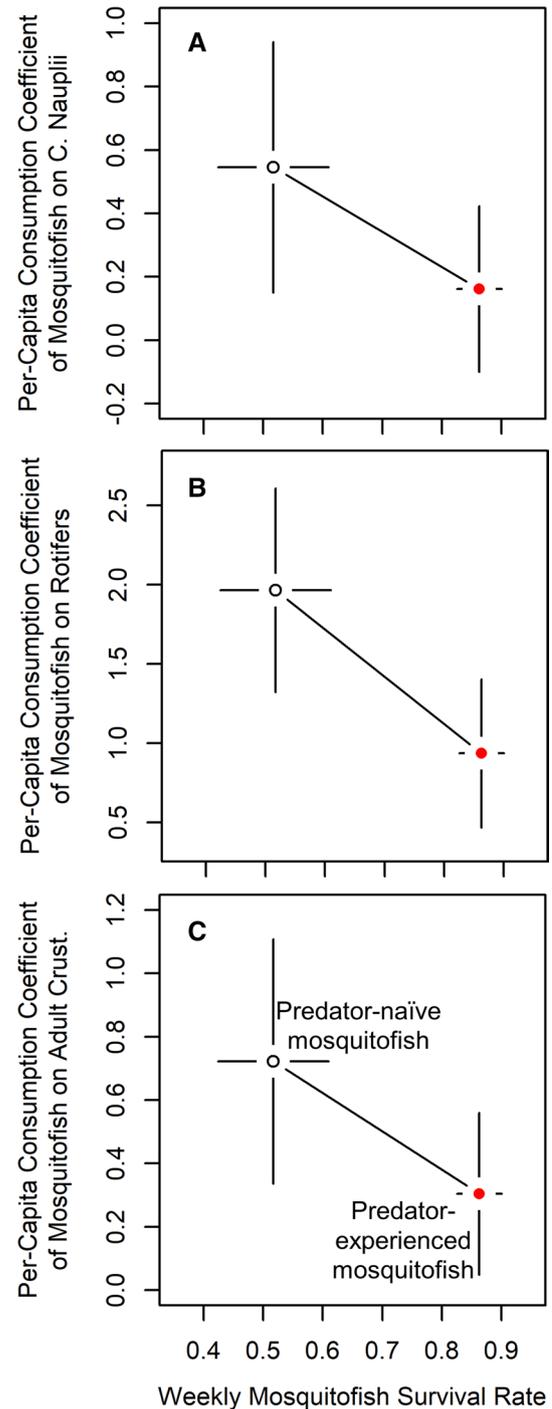


of predator introductions, shifting the cascade mechanism from density-mediated to trait-mediated as prey become more experienced. The degree to which this shift remains ecologically cryptic theoretically depends on the relative strength of opposing density (survival) and trait (feeding) mechanisms. In our experiment, these opposing mechanisms were roughly equal in effect size. The decrease in density-mediated effects was compensated by an increase in trait-mediated effects, leading the net strength of the cascade to remain about constant. This scenario represents a cryptic shift in the mechanism driving the trophic cascade. However, such complete compensation may not be present in all instances. Theoretically, the relative balance of density and trait effects should determine whether antipredator traits weaken classic density-mediated trophic cascades

(density > trait), cryptically replace them (density ≈ trait), or amplify them (density < trait). For predator introductions into communities with predator-experienced prey, trait-mediated processes may dominate trophic cascades from their onset (Carpenter et al. 1987). Thus, strong density-mediated trophic cascades are probably most-likely to occur when the added predator is a novel invasive to which prey are naïve (Kimbrow et al. 2009; Ferrari et al. 2015; Walsh et al. 2016). While mesocosm studies may distort the relative strengths of density- and trait-mediated interactions—by confining organisms to unusually small systems with artificially-stabilized resource dynamics (Preisser et al. 2009; Geraldi and Macreadie 2013)—this work nonetheless shows that cryptic trophic dynamics driven by prey experience are possible and follow predictable patterns. These distorted



**Fig. 4** Zooplankton densities were negatively related to mosquitofish densities when bass were present, with the slope of the relationship dependent on mosquitofish source. Mosquitofish from a predator-naïve source had a strong per-capita effect (i.e. consumption rate) on copepods nauplii (a), rotifers (b), and adult crustaceans (c), while mosquitofish from a predator-experienced source had a weak per-capita effect. Lines show general linear mixed model predictions for each source-type. Data from weeks 2–6 are pooled, with variation from time and mesocosm identity effects removed;  $N = 80$



**Fig. 5** Mosquitofish exhibited a feeding-survival tradeoff: predator-experienced mosquitofish had higher survival but lower consumption rates on copepods (a) and rotifers (b). Points are source-level estimates (i.e.  $L_S$  and  $C_S$  from Eqs. 2 and 3b, respectively). Bars indicate  $\pm 1$  standard error

interaction strengths may also explain why our bass-induced trophic cascades tended to follow hump-shaped trends, as the zooplankton may have surged in density after bass introduction, then experienced a density-dependent crash.

**Table 2** Mosquitofish had source-specific per-capita effects on some groups of zooplankton but not primary producers when bass were present

Dependent variable	Explanatory variable						
	Fish <sup>1/3</sup>			Fish <sup>1/3</sup> · experience			
	$\chi^2$	df	p	$\chi^2$	df	p	
All adult crustaceans	0.0122	1	0.91	3.67	1	<b>0.055</b>	
All copepods	0.11	1	0.74	10.5	1	<b>0.0012</b>	
Adult copepods	1.05	1	0.30	0.90	1	0.34	
Copepodites	0.49	1	0.48	0.40	1	0.53	
Copepod nauplii	0.21	1	0.65	3.93	1	<b>0.047</b>	
All cladocerans	0.025	1	0.87	2.01	1	0.16	
<i>Bosmina</i>	0.085	1	0.77	1.74	1	0.19	
<i>Daphnia</i>	0.17	1	0.68	0.13	1	0.72	
<i>Ceriodaphnia</i>	0.31	1	0.58	2.84	1	0.09	
Rotifers	2.67	1	0.10	6.01	1	<b>0.014</b>	
Chlorophyll <i>a</i>	0.41	1	0.52	0.94	1	0.33	
GPP	1.54	1	0.22	0.73	1	0.39	

Tests shown are likelihood ratio tests, conducted sequentially (fish, then fish · experience). Null model includes fixed time factor effect and random mesocosm identity effect.  $N=80$  for each model

Interestingly, when bass were absent, predator-experienced mosquitofish had greater short-term impacts on zooplankton (Fig. 2, Table 1). This trend suggests that predator-experienced mosquitofish may feed more aggressively in the absence of predators than predator-naïve mosquitofish (Walsh and Reznick 2008). However, this trend does not necessarily indicate that predator-experienced mosquitofish have higher fitness than predator-naïve mosquitofish in the absence of predators, as differences in metabolism and life-history may still make predator-naïve mosquitofish have higher fitness in the absence of predators (Reznick et al. 1990).

This work adds to the growing literature suggesting that intraspecific variation can generate or alter trophic cascades. Contemporary adaptation in upper trophic levels can cause cascading top-down effects on food webs (Ingram et al. 2012; Palkovacs et al. 2012; Walsh et al. 2012; Ousterhout et al. 2018; Start 2018). The rearranging of relative interaction strengths during a classic density-mediated trophic cascade can also alter selection pressures on lower trophic levels, driving contemporary adaptation (Wood et al. 2018). Prey adaptation at the population (Mooney et al. 2010) or community level (Fahimipour et al. 2017) can mediate the strength and reach of trophic cascades (Wood et al. 2018), and feed-back to impact predator success (Fryxell et al. 2019). Our work here demonstrates that prey adaptation not only affects the strength and extent of trophic cascades, but also the specific mechanisms underlying apparent cascades. Thus, future work should examine how patterns of prey adaptation along competition-defense tradeoffs extend to replicate populations within species and replicate species within trophic levels.

At an emergent systems level, cryptic shifts from density- to trait-mediated trophic cascades could serve as a stabilizing process in food webs. The increased survival of predator-experienced mosquitofish is a form of rescue dynamic (Gonzalez et al. 2013), effectively maintaining mosquitofish at higher densities, buffering them against numeric collapse and the potential extinction vortex of Allee effects (Gascoigne and Lipcius 2004). A more stable, defended mosquitofish resource may also prevent bass from self-extirpating through resource depletion (Yamamichi and Miner 2015). These outcomes imply weaker ecological interaction strengths between bass, mosquitofish, and zooplankton, and weaker interactions strengths are associated with greater overall food-web network stability (McCann et al. 1998; Neutel et al. 2002).

While we found strong evidence for effects of mosquitofish on zooplankton, we did not detect a measurable effect of mosquitofish experience on pelagic producers (Fig. 2, Table 1). This result could be because cladocerans, especially *Daphnia*, were uncommon in all mesocosms throughout the experiment (Fig. 2, Table 1). *Daphnia* are highly efficient grazers, and their reduction by mosquitofish is known to have large effects on the abundance and composition of pelagic phytoplankton (Hurlbert et al. 1972). Thus, with *Daphnia* comparatively rare throughout this experiment, effects of mosquitofish experience on zooplankton may not have been transmitted strongly to phytoplankton. Alternatively, changes in producer community composition (i.e. compensation) can sometimes prevent overall changes in producer biomass (Beckerman et al. 1997; Bell 2002; Tessier and Woodruff 2002; Sommer et al. 2003). Thus, we may have failed to detect compositional changes that might have occurred in the phytoplankton community.

Our results show that density- and trait-mediated effects are functionally interconnected through tradeoffs underlying the antipredator traits of prey, and their relative importance in trophic cascades can be mediated by prior prey population experience with predators. Here we found that increasing prey experience cryptically shifted the trophic cascade mechanism from density-mediated to trait-mediated. Our results suggest that debates about the dominant cascade mechanism in nature may be a false dichotomy, since traits that reduce feeding in the presence of predators also increase survival. It may therefore be profitable to broadly consider cascade mechanisms along a continuum of prey experience with predators.

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**Author contribution statement** DCF, EPP, and MTK designed the experiment. DCF, EPP, ZTW, MTK, KSS, and ERM carried out the experiment and collected the data. ZTW performed data analyses and led the writing of the manuscript.

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Compliance with ethical standards

**Conflict of interest** The authors declare no conflicts of interest.

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