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A. Mokany · R. Shine

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Abstract Tadpoles and mosquito larvae often co-occur, and may compete for scarce resources. However, competition between such distantly related organisms has attracted less scientific attention than have interactions among closely related taxa. We examined ecological interactions in two tadpole-mosquito systems in southeastern Australia, one from freshwater ponds (*Limnodynastes peronii* and *Culex quinquefasciatus*) and one from brackish-water habitats (*Crinia signifera* and *Ochlerotatus australis*). Diets of these tadpoles and mosquito larvae overlap considerably, potentially leading to competition for food. Laboratory experiments show that, in both study systems, mosquitoes reduced the growth rates of tadpoles, and tadpoles reduced the growth rates and survival of mosquito larvae. These negative effects were seen even at high food levels. Thus, our study suggests that tadpoles and mosquito larvae affect each other strongly, and do so via pathways other than simple consumptive competition. Because mosquitoes are important vectors for human diseases, the global decline in amphibian populations may have more impact on human health than has generally been anticipated.

Keywords *Crinia* · *Culex* · *Limnodynastes* · *Ochlerotatus* · Interphyletic competition

Introduction

Competitive interactions among organisms are widespread in natural ecosystems, and may often be important determinants of their species composition and persistence (Bronmark et al. 1991). Although the study of competition has thus been a major theme of ecological research for many decades (e.g. Lotka 1932), most studies in this

A. Mokany · R. Shine (✉)
School of Biological Sciences A08, University of Sydney,
NSW 2006, Australia
e-mail: rics@bio.usyd.edu.au
Tel.: +612-93513772
Fax: +612-93515609

field have focused on interactions between closely related species (Connell 1983; Diamond 1987; Gurevitch et al. 1992). Indeed, the idea that competition between sibling taxa will often be intense because of their close morphological and behavioural similarities dates from Darwin (1859). Nonetheless, competition may also occur between organisms that are related only distantly and, thus, share few phenotypic similarities (e.g. Alford 1999; Brown and Davidson 1977; Carpenter 1979; Hurlbert et al. 1986; Morin et al. 1988).

Because of logistical constraints, competitive effects are easiest to assess in small, discrete habitat patches with relatively low species diversity. Ephemeral ponds offer an ideal opportunity in this regard. The habitat itself is discrete, and the food resources within it constrain the development of aquatic larvae which must grow and metamorphose before the pond dries (Newman 1994). Two of the most abundant and conspicuous components of the fauna within such ephemeral habitats are tadpoles and mosquito larvae (Blaustein and Margalit 1994, 1996). Both are primarily herbivorous (Alford 1999; Bern and Dahl 2000; Mokany 2001; Peterson and Boulton 1999).

Herbivorous tadpoles consume a wide range of organic material (Farlowe 1928), including green algae (Jenssen 1967), unicellular chlorophytes (Kupferberg et al. 1994), cyanobacteria (Seale and Beckvar 1980), faecal pellets (Steinwascher 1979) and organic detritus (Seale and Wassersug 1979). Tadpoles use both suspension feeding and scraping of organic matter from surfaces (Alford 1999; Kenny 1969). They are effective grazers, capable of reducing algal abundance (Rosenfeld 1997). This can have both positive and negative effects on other organisms (Morin 1983). Positive effects have been demonstrated for dipteran larvae raised with tadpoles (Osborne and McLachlan 1985). The tadpoles consumed algae at the surface of the water column and made them available to the bottom-dwelling dipteran larvae through their faecal pellets. This effectively gave the dipteran larvae access to resources that were otherwise unavailable to them (McLachlan 1981, 1985). However, most studies on this topic have demonstrated negative effects of tadpoles

feeding on other organisms. For example, intraspecific competition between tadpoles is more intense if food supply is reduced (Griffiths et al. 1993; Wilbur 1997). In addition, interphyletic competitive interactions between tadpoles and snails are caused by the tadpoles limiting the amount of food available (Bronmark et al. 1991).

Like tadpoles, mosquito larvae feed on a wide range of organic matter, including bacteria, detritus, protozoans and algae (Chessman 1986; Hart 1985; Walker et al. 1988, 1991). A recent study demonstrated that mosquito larvae did not discriminate between feeding on polystyrene beads versus planktonic algae (Bern and Dahl 2000). The feeding mechanisms of mosquito larvae are as diverse as their diets (Merritt and Craig 1987; Rashed and Mulla 1990). For example, *Culex* spp. are mainly planktotrophic, spending most of the time suspension-feeding with their siphons attached to the air-water interface (Widahl 1992). In contrast, *Ochlerotatus* spp. generally feed at the base of the water column, with younger larvae devoting less time to feeding than do later instars (Merritt et al. 1992).

Preliminary evaluation of the gut contents of the tadpoles (*Limnodynastes peronii* and *Crinia signifera*) and their co-occurring mosquito larvae (*Culex quinquefasciatus* and *Ochlerotatus australis*) have revealed that they have a high dietary overlap. Both these tadpoles and mosquito larvae consume largely algae and bacteria (Mokany 2001). Here, we investigated the potential ecological interactions between these species for food, using replicated artificial ponds within the laboratory. There was no evidence that the tadpoles used in this study consumed mosquito larvae (Mokany 2001) so that direct predation was unlikely to influence the results. Our primary aims in conducting this study were: (1) to determine whether or not these species negatively affect each other's rates of growth and survival, and (2) if so, to see whether such competitive interactions are consumptive (and, thus, mediated by food supply) or alternatively, involve other competition mechanisms.

Materials and methods

Study species

We studied two systems, one in freshwater ponds (*L. peronii* plus *Culex quinquefasciatus*), and one in brackish-water pools close to the high-tide line (*Crinia signifera* plus *O. australis*):

1. The striped marsh frog (*L. peronii*) is a medium-sized frog (to 65 mm) common on the east coast of Australia (Cogger 2000). It mainly breeds from August to March, laying 700–1,000 eggs in a foam egg mass at the edge of water bodies such as freshwater creeks and ponds (Robinson 1996). The tadpoles of this species commonly co-occur with the mosquito species *Culex quinquefasciatus* in backyard ponds, creeks and streams (Mokany 2001). *Culex quinquefasciatus* has a global distribution and inhabits all states of mainland Australia (Russell 1993). This mosquito species also breeds from August to March, laying egg rafts on the surface of stagnant freshwater ponds. The larvae of this species can complete development in 7–12 days (Mpho et al. 2000).

2. The common eastern toadlet (*Crinia signifera*) is a small (35 mm) terrestrial frog from a variety of habitats within Queensland, New South Wales, Victoria, South Australia and Tasmania. The larvae of this species inhabit both permanent and ephemeral ponds (Cogger 2000) and commonly co-occur with larvae of the mosquito *O. australis* in small coastal rock ponds (Mokany 2001). This mosquito inhabits vast areas of coastal Australia and breeds year-round, depositing its eggs above the high-tide mark on rock platforms of the coast (Russell 1993). Larvae of these mosquitoes are aggressive towards other organisms and feed on animal as well as plant material (Mokany 2001).

Competition experiments

From October to November 2000, we conducted a series of experiments in the laboratory using 1.5-l (10 cm×10 cm×15 cm) polyethylene containers as artificial ponds. These containers were well within the size range of ponds that naturally contain both tadpoles and mosquitoes (Mokany 2001). To each tub we added 1 l of aged tap water (Aqua-pet water ager), 100 g aquaria gravel, and floating fish pellets (I.M.P.S). We assigned three treatments, each with three food levels—low (one pellet per day), medium (two pellets per day) and high (three pellets per day)—to these ponds, in a Latin square formation.

The numbers of tadpoles and mosquito larvae used per container differed between the systems because of differences in their abundances in natural water bodies (Mokany and Shine 2002b). The three treatments for *Crinia signifera* and *O. australis* were: (1) 3 early-stage tadpoles (stage 25; Gosner 1960), (2) 20 first-instar mosquito larvae, and (3) 3 early-stage tadpoles plus 20 first-instar mosquito larvae. For *L. peronii* and *Culex quinquefasciatus*, the treatments were: (1) 5 early-stage tadpoles (Gosner stage 25), (2) 20 first-instar mosquito larvae, and (3) 5 early-stage tadpoles plus 20 first-instar mosquito larvae. Each treatment was replicated five times. We weighed and measured the tadpoles prior to experimentation. We established the wet weight of the tadpoles by transferring tadpoles via a sieve into a petri dish full of water, onto the pan of a digital balance. We measured the tadpoles with digital calipers (±0.01 mm) to record length (from snout to tail-tip) and maximum body width.

We checked the containers daily for mosquito pupae, and any pupae were transferred to a separate container to metamorphose. This removal of pupae should not influence competitive interactions because the pupae do not feed or excrete. We froze the metamorphosed adult mosquitoes to enable later measurement of wing sizes. We terminated the experiment after 25 days, as by this time most mosquito larvae had either died or pupated. We then re-weighed the tadpoles and recorded their final length and width. The measurements taken were converted to the mean percentage mass change, percentage length change and percentage width change of the three tadpoles since the beginning of the experiment.

At the end of experimentation, we calculated the percentage of mosquitoes that had pupated, the duration of their larval periods (day to pupation from the beginning of experimentation), their percentage survival and their wing sizes (separately for male and female mosquitoes). We measured wing size from the alular notch to the tip of the wing margin excluding wing scales.

Data analysis

We analysed our results using the program Statview 5 (SAS Institute 1998). All percentage data were transformed by arcsin square root prior to analysis. Due to the large number of dependent variables that we measured, conducting separate statistical tests on each variable would raise issues of artificially "significant" results simply due to the number of tests conducted. Unfortunately, methods to remedy this situation (such as applying Bonferroni "correction factors") are themselves prone to considerable subjectivity (Cabin and Mitchell 2000; Snedecor and Cochran 1980).

Therefore, we combined the data from both study systems and conducted multivariate ANCOVA (MANCOVA) separately for tadpoles and mosquito larvae. The probability values from these analyses offer robust evidence on the significance of results, because they are based on single comparisons that use all available data.

Results

Competition experiments

The MANCOVA for tadpoles included two factors: tadpole species and the presence/absence of mosquito larvae. Food level was included as a covariate (a continuous variable) rather than as a nominal factor, because of the clear quantitative relationship among treatment levels (one, two or three pellets per day). Analyses that included food level as a nominal rather than continuous variable yielded virtually identical conclusions. The dependent variables were proportional changes in the length, width and mass of tadpoles over the course of the experiment. The MANCOVA revealed that tadpole growth rates overall were higher when more food was available, and were depressed by the presence of mosquito larvae (Table 1). Overall growth rates did not differ significantly between the two species of tadpoles, but the two species responded differently to variations in food supply and the presence of mosquitoes (Table 1). Importantly, however, the growth rates of tadpoles were not significantly affected by the interaction between mosquito presence and food supply, nor by the three-way interaction between food level, mosquito presence and tadpole species (Table 1).

The MANCOVA for mosquito larvae included mosquito species and presence/absence of tadpoles as factors, food level as a covariate, and dependent variables of the number of days to pupation, the proportion of larvae pupating, the proportion surviving, and male wing sizes. No female mosquitoes emerged from some treatments, so that we could not include female wing size in the MANCOVA. As for the MANCOVA on tadpoles
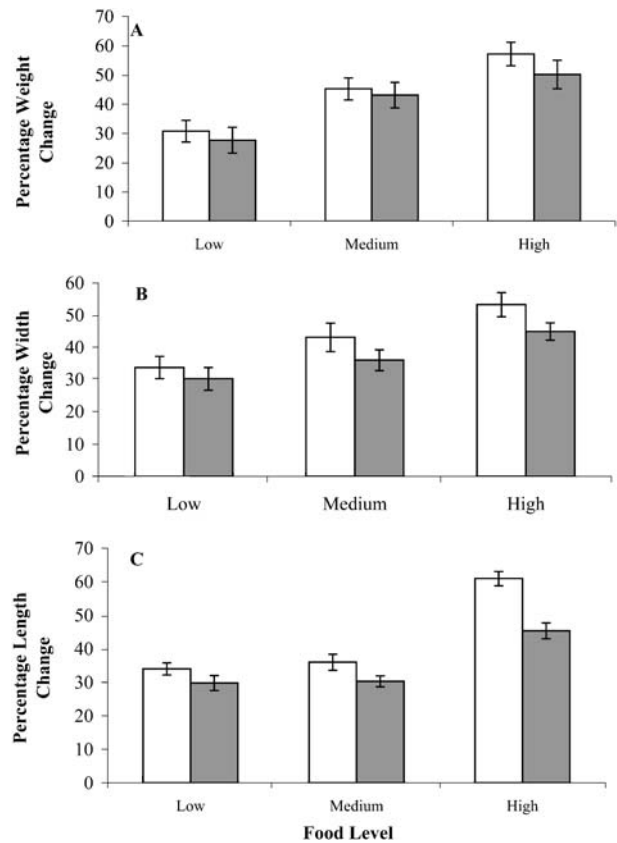
Fig. 1A–C Effects of the level of food and presence of mosquito larvae on the growth rates of tadpoles (*Limnodynastes peronii*). The graphs show mean values (±SE) for percentage growth measured for *L. peronii* raised without mosquito larvae (*unfilled histograms*), and *L. peronii* tadpoles raised with *Culex quinquefasciatus* mosquito larvae (*shaded histograms*) at various food levels. The histograms represent: **A** percentage weight change; **B** percentage width change; **C** percentage length change of the tadpoles for the various treatments. The *x*-axis represents food level

(above), the attributes of mosquitoes were affected by food supply and the presence of tadpoles, and differed between the two mosquito species (Table 1). The variables we measured on mosquitoes were also influenced by the three-way interaction between mosquito species, food supply and tadpole presence, and lower-level interaction terms were statistically significant as well (Table 1).

In summary, tadpoles in both study systems grew more rapidly when given more food, and less rapidly in the presence of mosquito larvae (Fig. 1). Effects on mosquitoes were more complex, and differed between the two study systems. In freshwater ponds (*L. peronii* and *Culex quinquefasciatus*), food supply affected some but not all traits of mosquito larvae (Fig. 2). The amount of food had no significant effect on the day to pupation, female wing size or percentage pupation, but male wing size and percentage survival were reduced in the low-food treatment compared to the high-food treatment (Fig. 2). The presence of tadpoles did not affect day to pupation or female wing size for *Culex quinquefasciatus* mosquitoes,

Table 1 Results of multivariate analysis of covariance (MANCO-VA) on phenotypic traits of tadpoles and mosquitoes in laboratory competition experiments. The study species were *Limnodynastes peronii* and *Culex quinquefasciatus* from freshwater ponds, and *Crinia signifera* and *Ochlerotatus australis* from brackish-water habitats. Food supply was used as a covariate. For tadpoles, *F*-values have 3,230 *df*; for mosquitoes, *F*-values have 4,38 *df*. Table shows *P*-values from Wilk's Lambda. **Boldface** shows *P*<0.05

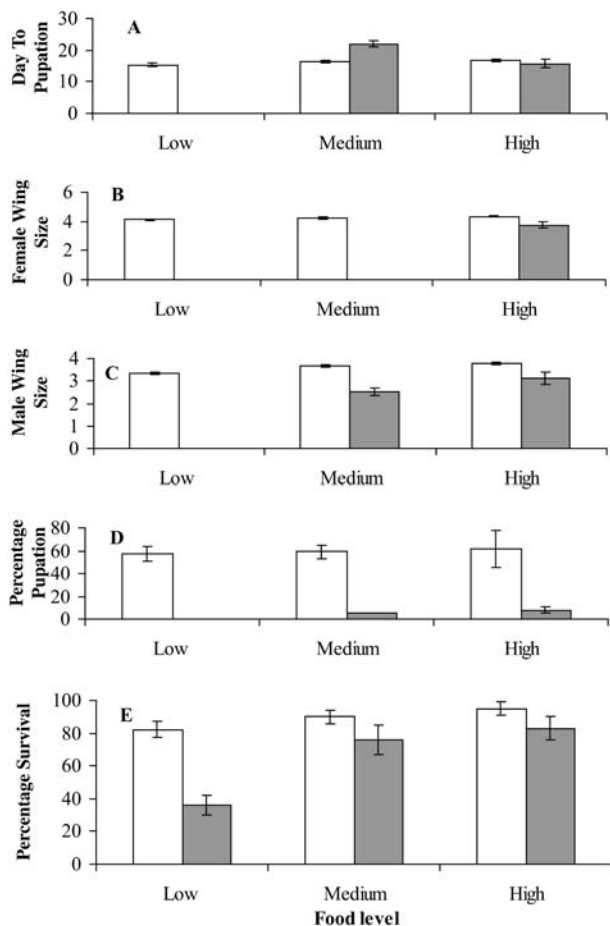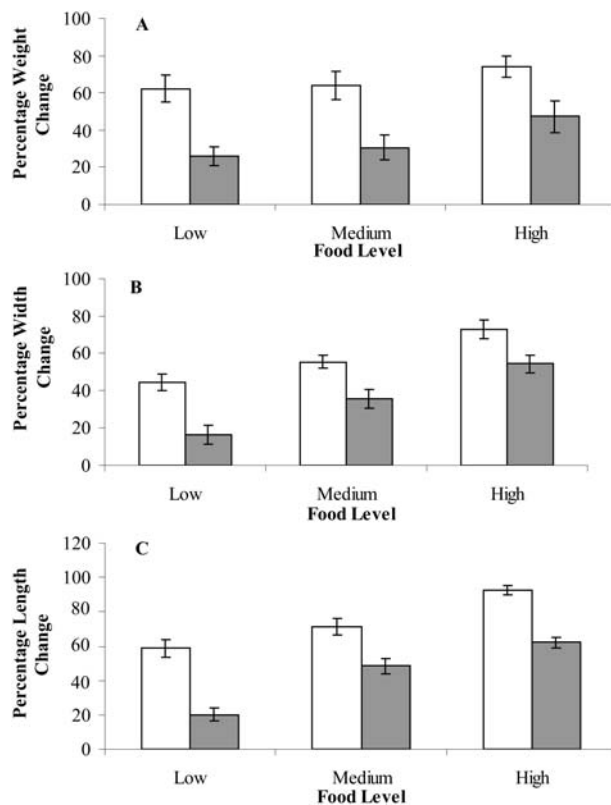| Variable	Tadpoles		Mosquitoes	
	F	*P*	*F*	*P*
Species	2.35	0.07	5.43	**0.002**
Presence of competing taxon	4.82	**0.003**	8.58	**0.0001**
Food supply	69.11	**0.0001**	9.33	**0.0001**
Species*competitor	5.93	**0.001**	7.73	**0.0001**
Species*food	7.84	**0.0001**	2.45	0.06
Competitor*food	1.25	0.29	3.85	**0.01**
Species*competitor*food	0.68	0.56	3.40	**0.02**

Fig. 2A–E Effects of food level and presence of tadpoles on the traits of the mosquito *Culex quinquefasciatus*. The graphs represent mean values (±SE) for traits measured for *C. quinquefasciatus* mosquito larvae raised without tadpoles present (*unfilled histograms*), and *C. quinquefasciatus* raised with *Limnodynastes peronii* tadpoles (*shaded histograms*). The histograms represent: **A** day to pupation; **B** female wing size; **C** male wing size; **D** percentage pupation; **E** percentage survival of the mosquito larvae for the experimental period. The *x*-axis represents the experimental food level

Fig. 3A–C Effects of the level of food and presence of mosquito larvae on the growth rates of tadpoles (*Crinia signifera*). The graphs show mean values (±SE) for percentage growth measured for *Crinia signifera* raised without mosquito larvae present (*unfilled histograms*), and *Crinia signifera* tadpoles raised with *Ochlerotatus australis* mosquito larvae (*shaded histograms*) at various food levels. The histograms represent: **A** percentage weight change; **B** percentage width change; **C** percentage length change of the tadpoles for the various treatments. The *x*-axis represents food level

but affected all other traits. For example, male wing size, percentage pupation and percentage survival were lower in the treatments raised with tadpoles (Fig. 2).

In brackish-water ponds (*Crinia signifera* and *O. australis*), food supply affected all of the measured traits of *O. australis* except for percentage survival (Figs. 3, 4). The mosquitoes in the low-food treatments pupated later, often failed to pupate and were smaller if they did so, than were mosquitoes in the high-food treatments (Fig. 4). The presence of tadpoles did not affect day to pupation or percentage pupation of the mosquitoes, but wing sizes and percentage survival were reduced when the mosquitoes were raised with tadpoles (Fig. 4).

Discussion

Increasing the supply of food in our experiments accelerated the growth of both the tadpoles and the mosquitoes with or without competitors. However, the presence of competitors depressed the growth rates of both the tadpoles and the mosquito larvae, even at high food levels. These results suggest that tadpoles and mosquito larvae can potentially compete for food, and that they do indeed suppress each other in laboratory "ponds". However, the mechanism for this suppression involves more than simple consumptive competition.

Tadpoles of both study species were affected by the level of food they were given, as well as by interactions with mosquito larvae. *L. peronii* and *Crinia signifera* tadpoles experienced reduced growth at low food levels, indicating (unsurprisingly) that the abundance of food can influence the growth and development of tadpoles (Figs. 1, 3). This finding is consistent with previous studies; tadpoles fed reduced amounts of food (Griffiths et al. 1993; Newman 1994, 1998) or low-quality food (Kupferberg 1997) grow at reduced rates compared to those
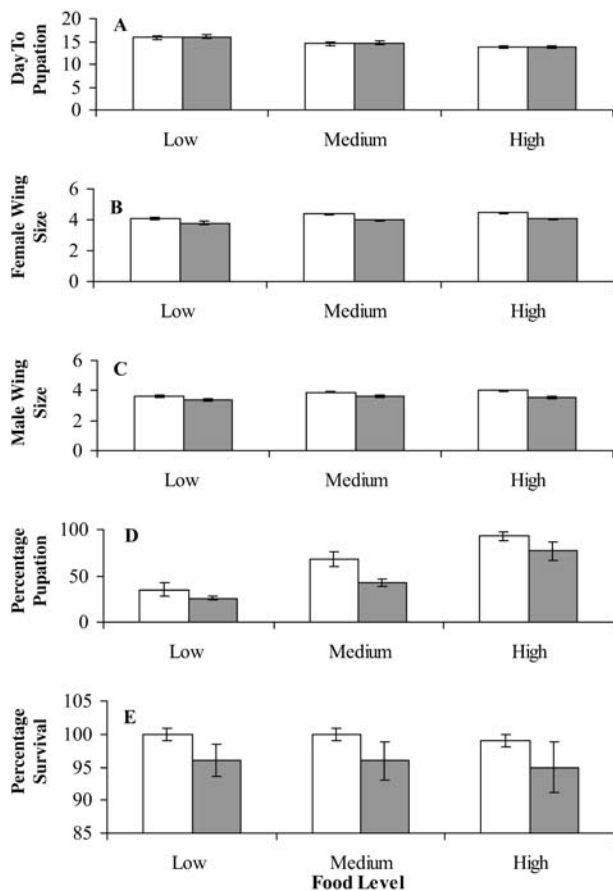
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