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The role of gape-limitation in intraguild predation between endangered Mohave tui chub and non-native western mosquitofish

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Abstract – Intraguild predation (IGP) is a mechanism that may facilitate the co-existence of native species with non-native invasive species. We conducted laboratory predation trials to assess the role of predator gape-limitation in the context of IGP between the endangered Mohave tui chub (*Siphateles bicolor mohavensis*) and invasive western mosquitofish (*Gambusia affinis*). Larval tui chubs had significantly lower ($\chi^2 = 74.74$; $P < 0.001$) survival in the presence of female mosquitofish (10.0%) than in the presence of male mosquitofish (73.3%). Reciprocally, adult tui chubs preyed upon adult mosquitofish, causing a significantly lower ($\chi^2 = 11.33$; $P < 0.001$) survival for male mosquitofish (60%) compared to female mosquitofish survival (96.7%). Vulnerability modelling revealed that mosquitofish with a body depth < 4.6 mm and a larval tui chub with a body depth < 1.2 mm were completely vulnerable to predation by adult Mohave tui chub and adult mosquitofish, respectively. IGP in this study system is size-structured based on gape-size limitation and may have some conservation implications for the recovery of endangered Mohave tui chub. Our findings also provide an important caveat to the dogmatic view of mosquitofish as a threat whenever they invade. It is important to note that many previous studies that reported negative impacts of mosquitofish involved native species with relatively small body sizes, often the same size as mosquitofish.

Key words: mosquitofish impact; invasive mosquitofish; co-existence; gape-size limitation; vulnerability modelling

Introduction

Predation is one of the most widespread ecological interactions shaping community structure (Sih et al. 1985; Diehl 1992; Post et al. 2008) as well as life-history evolution of interacting organisms (Reznick et al. 1990; Stibor 1992; Ingram et al. 2012). However, the relative roles of predator and prey are not static and may change with individuals of a single species acting as both predator and prey depending on their age and size (Polis et al. 1989; Polis & Holt 1992). Such *intraguild predation* (IGP) is a widespread phenomenon in nature (Polis & Holt 1992; Arim & Marquet 2004); nevertheless, a few studies have evaluated how IGP may affect the co-existence of native and non-native species (but see Taniguchi et al. 2002; Arim & Marquet 2004).

In theory, IGP may facilitate invasion dynamics, but IGP may also facilitate the co-existence of native species with non-natives. Taniguchi et al. (2002) showed IGP provided a competitive advantage for non-native, stream-dwelling rainbow trout (*Oncorhynchus mykiss*) over native, anadromous masu salmon (*O. masou*), facilitating rainbow trout invasion in Japanese streams. By contrast, size-structured IGP may facilitate co-existence of endangered Mohave tui chub (*Siphateles bicolor mohavensis*) with non-native western mosquitofish (*Gambusia affinis*; Stockwell & Henkanaththegedara 2011; Henkanaththegedara 2012). In both case studies, IGP appeared to be size-structured based on predator gape-size limitation.

The vulnerability of prey is often limited by the gape-size of predators relative to their prey (Hambright 1991, 1994; Webb and Shine 1993;

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Nilsson & Bronmark 2000; Magnhagen & Heibo 2001). For example, Magnhagen & Heibo (2001) reported a positive correlation between gape-size of northern pike (*Exos lucius*) and body depth of its piscine prey. Predation risk is reduced as the prey grows and body depth exceeds the predator's maximum gape-size (Hambright et al. 1991; Nilsson et al. 1995). Therefore, predator gape-size and prey body depth may have important implications in a system where predation is structured based on relative body sizes of predator and prey.

We previously reported reciprocal predation between endangered Mohave tui chub and non-native western mosquitofish, where adult tui chubs preyed on adult and juvenile mosquitofish while mosquitofish preyed on eggs and larvae of tui chubs (Stockwell & Henkanaththegedara 2011; Henkanaththegedara 2012). Because these two species occupy the same feeding guild (88% dietary overlap; Henkanaththegedara 2012), this case of reciprocal predation between Mohave tui chub and western mosquitofish meets the criteria of IGP.

Two lines of evidence suggest that IGP between these two species is structured by gape-size limitation. First, male mosquitofish, which is the smaller sex of this dimorphic species, had very low survival (3%) compared to female mosquitofish (34%) in the presence of Mohave tui chub. Second, female mosquitofish that survived in the presence of adult tui chubs were relatively large. Reciprocally, mosquitofish preyed upon Mohave tui chub larvae, which is also likely to be gape-limited (Mills et al. 2004; Henkanaththegedara 2012).

Here, we report the results of a series of laboratory predation trials designed explicitly to assess gape-limitation in the context of IGP between Mohave tui chub and western mosquitofish. We also present a prey vulnerability model (Hambright et al. 1991) that allows us to evaluate how gape-size-limited predation affects each fish population.

Materials and methods

Tui chub predation experiment

Predation on adult western mosquitofish was assessed using adult Mohave tui chubs (sexually monomorphic) as candidate predators. We tested both adult male and female mosquitofish as candidate prey because mosquitofish are sexually dimorphic in size. Sixty adult Mohave tui chubs used in this experiment were collected in 2009 from Lake Tuendae ($N = 23$), Camp Cady ($N = 27$) and MC Spring ($N = 10$; Table 1) and transported to North Dakota State University (NDSU). Western mosquitofish were collected from Deppe Pond at the Lewis Center for Academic Excellence in Apple Valley, California, and transported to NDSU.

Sixty 37.8-l glass aquaria were used as experimental chambers. Three vertical sides of each aquarium were covered with black plastic sheets to avoid any visual interference among tanks. Aquaria were continuously aerated by a centrally suspended aerator in each tank. A full spectrum light source was placed 35 cm above each tank, and a light cycle of 16-h light/8-h dark was used.

This experimental design provided 30 replicates, using either male mosquitofish or female mosquitofish allowing an assessment of tui chub predation on mosquitofish by sex. Mohave tui chub predators were measured for total length (nearest 1 mm) and gape-size (nearest 0.01 mm). Tui chub gape-size was

Table 1. Mean size of Mohave tui chub (*Siphateles bicolor mohavensis*) and western mosquitofish (*Gambusia affinis*) utilised for predation experiments. Adult Mohave tui chubs were collected in 2009 from Lake Tuendae ($N = 23$), Camp Cady ($N = 27$) and MC Spring ($N = 10$). Larval tui chubs were provided from a captive stock at Mojave National Preserve. All western mosquitofish were collected from Lake Tuendae. One standard error is indicated in parenthesizes.

|	Prey treatment				
Experiment/measurement	♂ mosquitofish	♀ mosquitofish	N	t-value	P-value
Mohave tui chubs as predators					
Adult Mohave tui chub					
Total length (mm)	101.70 (±2.68)	105.50 (±2.43)	30	−1.049	>0.05
Gape-size (mm)	6.24 (±0.20)	6.54 (±0.20)	30	−1.057	>0.05
Adult western mosquitofish					
Total length (mm)	30.00 (±0.29)	40.72 (±0.79)	30	−12.742	<0.001
Body depth (mm)	6.22 (±0.06)	8.31 (±0.17)	30	−11.404	<0.001
Mosquitofish as predators					
Adult western mosquitofish					
Total length (mm)	26.02 (±0.66)	38.12 (±0.88)	30	−11.013	<0.001
Gape-size (mm)	2.00 (±0.04)	3.43 (±0.09)	30	−14.590	<0.001
Larval Mohave tui chub					
Total length (mm)	13.78 (±0.48)	14.67 (±0.54)	30	−1.243	>0.05
Estimated body depth (mm)	2.30 (±0.09)	2.47 (±0.10)	30	−1.243	>0.05
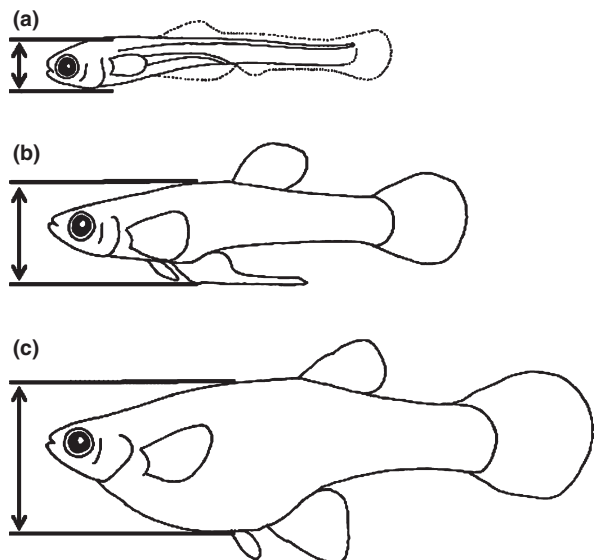
Fig. 1. Body depth measurements of a Mohave tui chub larvae (*Siphateles bicolor mohavensis*) (a), a mature male (b) and a pregnant female (c) of western mosquitofish (*Gambusia affinis*).

measured from the ventral side (tui chubs have a subterminal mouth) as the linear distance between posterior limit of maxilla with mouth fully closed. Mosquitofish were measured for total length and body depth (nearest 0.01 mm). Female mosquitofish body depths were measured at the base of pelvic fins, while male mosquitofish body depths were measured at the deepest point of the gonopodial base (Fig. 1). Measured mosquitofish were kept in individual containers prior to introduction into aquaria. Mohave tui chubs assigned between the two treatments did not significantly differ in total length ($t = -1.05$; $P > 0.05$) and gape-size ($t = -1.06$; $P > 0.05$). As expected, female mosquitofish were significantly larger in total length ($t = -12.74$; $P < 0.001$) and gape-size ($t = -11.40$; $P < 0.001$) compared to male mosquitofish (Table 1).

For each predation trial, an adult tui chub was deprived of food for 24-h prior to being placed in a randomly selected aquarium. After a 4-h acclimation period, a single mosquitofish was introduced into each aquarium. Survival was monitored every 3-h over the 72-h test period, and time to death (TTD) was recorded for each mosquitofish.

Mosquitofish predation experiment

Mosquitofish predation on larval tui chubs was assessed using either adult male or adult female mosquitofish as candidate predators and Mohave tui chub larvae as candidate prey (Table 1). For these trials, mosquitofish were obtained from a commercial stock from Arizona (Arizona Aquatic Gardens; www.azgardens.com). Mohave tui chub larvae were provided by

Mojave National Preserve, California (D. Hughson, Mojave National Preserve, Barstow, California).

Small 4.7-l opaque plastic containers were used as experimental chambers. Chambers were not aerated because of the short experimental time period and low fish density. This experiment consisted of two predator treatments, male and female mosquitofish, with 30 replicates each. In addition, we included a control of Mohave tui chub larvae maintained in the absence of mosquitofish ($n = 28$), to account for any mortality of tui chub larvae because of handling stress.

Mosquitofish predators were measured for total length and gape-size (nearest 0.01 mm). Mosquitofish gape-size was measured dorsally due to superior nature of their mouths. Male mosquitofish were significantly smaller in total length ($t = -11.01$; $P < 0.001$) and gape-size ($t = -14.59$; $P < 0.001$) compared to female mosquitofish (Table 1).

Tui chub larvae were measured for total length (nearest 0.01 mm) using digital callipers, while resting on a watch glass filled with a small amount of water. Subsequently, tui chub larvae were monitored for at least 3-h following measurements to assess any handling associated mortality. Body depths were difficult to measure on live tui chub larvae. Therefore, we measured a sample of Mohave tui chub larvae voucher specimens to derive a regression formula of body depth on total length [body depth = (0.1986 × total length)−0.4251; $r^2 = 0.96$; $N = 148$]. Mohave tui chub larval body depth was measured at the middle of the head (Fig. 1). The average total length of Mohave tui chub larvae exposed to mosquitofish predation did not significantly differ between male and female mosquitofish treatments ($t = -1.24$; $P > 0.05$; Table 1).

Adult mosquitofish were deprived of food for 24 h prior to being placed in a randomly selected experimental chamber. After the 4-h acclimatisation period, a single tui chub larva was introduced into each experimental chamber and its survival was monitored every 15 min over a 4-h test period and TTD was recorded for each tui chub larva. In a few cases, tui chub larvae died during the trial but were not consumed. These trials were excluded from the survival analyses.

Statistical analysis

We conducted all statistical analyses using R statistical software program version 2.11.0 (R Development Core Team 2010). Package *survival* was utilised to analyse prey survival (Therneau & Lumley 2009). This package uses the *Surv()* function to simultaneously evaluate TTD and the censoring information (0 = live; 1 = dead; Maindonald & Braun 2010).

Survival functions were estimated with Kaplan–Meier survival estimate (*survfit* function) using TTD data. Hazard functions for treatment groups were tested using Cox proportional hazards model (*coxph* function).

The ratio between prey body depth and predator gape width (here after depth/gape ratio) was utilised to assess gape-size limitation. In theory, predators could not consume prey larger than their gape-size (Hambright et al. 1991); hence, the depth/gape ratio should be ≤ 1.0 for prey consumed and >1.0 for survivors. We ran separate one-sample, two-tail *t*-tests (*t.test* function) with depth/gape ratios using a null hypothesis of $\mu = 1$ to detect any significant deviations from 1 (when prey body depth = predator gape-size) after testing data for normality with a Shapiro–Wilk normality test (*shapiro.test* function). Prey that were possibly killed by the predator but not consumed were excluded from these analyses (mosquitofish as predator, $N = 5$; tui chubs as predator, $N = 1$).

Vulnerability modelling

Hambright et al.'s (1991) vulnerability model assumes that predator gape-size and prey body depth are the critical factors that determine the prey size ingested by a predator. Relative vulnerability of prey (V) to predation was estimated as a function of prey body depth (d) and the frequency of predators' gape-size (W) in the predator population.

$$V_d = 1 - \sum_{w=0}^{d} W$$

Prey with body depths larger than the gape-size of the largest individual of predator population were considered to be unavailable for predation (i.e., $V = 0$). However, prey with body depths smaller or equal to the gape-size of the smallest individual of the predator population were considered to be completely vulnerable to all the predators in the community (i.e., $V = 1$). The prey with intermediate body depths are vulnerable to a proportion of the predator population depending on the body depth ($0 < V < 1$; Hambright et al. 1991).

Relative vulnerabilities of adult mosquitofish to tui chub predation and larval tui chub to adult mosquitofish predation were determined using the cumulative gape-size frequency distributions of adult tui chubs and adult mosquitofish, respectively. To obtain the gape-size distribution of the Lake Tuendae tui chub population, we first ran a regression of gape-size on total length for a sample of 114 preserved Mohave tui chub specimens collected from four tui chub habitats (body depth = $(0.0734 \times$ total

Table 2. Size of Mohave tui chub (*Siphateles bicolor mohavensis*) and western mosquitofish (*Gambusia affinis*) utilised for vulnerability modelling. Adult Mohave tui chub total lengths were measured in March 2009 from Lake Tuendae population, and gape-sizes were estimated using a regression of gape-size on total length. All western mosquitofish were collected from Lake Tuendae.

S	N	Average (±SE)	Range
Mohave tui chub			
Adults			
Total length (mm)	3651	88.78 (±0.34)	55.0–309.0
Estimated gape (mm)	3651	6.56 (±0.02)	4.08–22.73
Larvae			
Total length (mm)	178	15.77 (±0.52)	6.19–44.67
Depth (mm)	178	2.70 (±0.10)	3.59–10.30
Western mosquitofish			
Females			
Total length (mm)	90	32.30 (±0.56)	21.63–45.38
Gape (mm)	90	2.76 (±0.05)	1.74–4.16
Depth (mm)	90	6.67 (±0.18)	3.59–10.30
Males			
Total length (mm)	59	25.30 (±0.25)	20.54–29.20
Gape (mm)	59	1.83 (±0.03)	1.19–2.46
Depth (mm)	59	5.06 (±0.07)	3.77–6.01

length) $+ 0.0479$; $r^2 = 0.8466$; Henkanaththegedara 2012). We then used this regression to estimate the gape-size for Mohave tui chubs ($N = 3651$) that were measured for total length during a mark–recapture study at Lake Tuendae in March 2009 (Table 2). The estimated gape-size distribution for Mohave tui chub adults was used to generate the vulnerability curve. We then plotted the body depth distribution for male and female mosquitofish under the curve to evaluate the relative size-specific vulnerabilities (Fig. 3a).

Relative vulnerabilities of larval tui chubs to mosquitofish predation were estimated using the gape-size distributions of adult male and female mosquitofish collected from Lake Tuendae (females = 90; males = 59; Table 2). The gape-size distribution for adult male mosquitofish and adult female mosquitofish were used to generate the respective vulnerability curves. We did not plot the larval size distribution because these data are not available and because each cohort of larval tui chubs will experience reduced vulnerability as they grow and eventually exceed the gape-size of mosquitofish.

Results

Tui chub predation experiment

Survival in the presence of tui chubs was significantly lower ($\chi^2 = 11.33$; d.f. = 1; $P < 0.001$) for male mosquitofish (60.0%; 95% CI: 44.8–80.4%) than for female mosquitofish (96.7%; 95% CI: 90.4–100.0%; Fig. 2a). The average depth/gape ratio for male mosquitofish consumed by tui chub predators (0.91 ± 0.03; $N = 12$) was significantly lower than
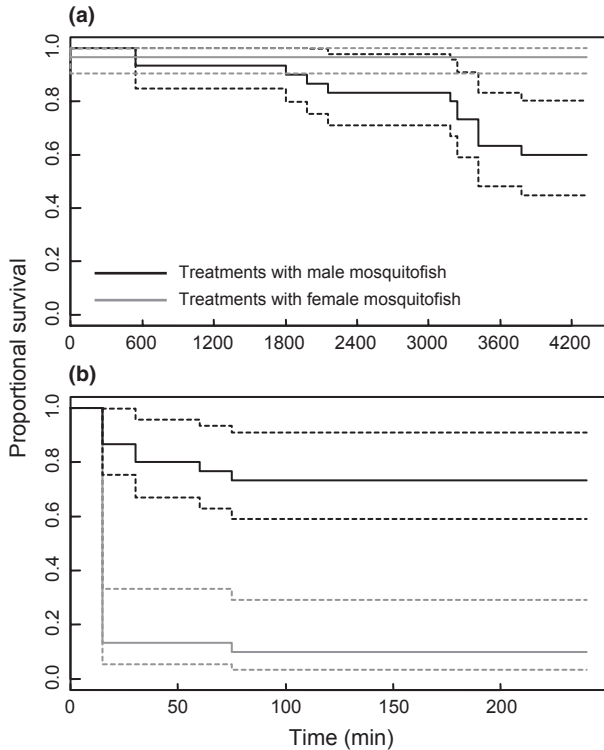
Fig. 2. Kaplan–Meier estimates of proportional survival of prey during predation trials for (a) adult western mosquitofish (*Gambusia affinis*) prey with adult Mohave tui chub (*Siphateles bicolor mohavensis*) as predators and (b) Mohave tui chub larval prey with adult western mosquitofish as predator. Solid lines indicate Kaplan–Meier proportional survival function, and dashed lines indicate 95% confidence intervals. Black and grey lines indicate the treatments with male and female mosquitofish, respectively.

1.0 ($t = -3.13$; d.f. = 11; $P = 0.0096$), whereas the depth/gape ratio for male mosquitofish survivors (1.11 ± 0.05; $N = 18$) was significantly greater than 1.0 ($t = 2.22$; d.f. = 17; $P = 0.406$). Furthermore, 29 of 30 female mosquitofish survived the experiment, and their average depth/gape ratio (1.31 ± 0.06) was significantly higher than 1.0 ($t = 5.14$; d.f. = 28; $P = 1.86$ e-5). The single nonsurviving female mosquitofish had a depth/gape ratio of 1.42 (killed but not consumed).

Mosquitofish predation experiment

Tui chub larval survival in the absence of mosquitofish was 100%, suggesting that handling stress was limited. Mohave tui chub larval survival was significantly lower ($\chi^2 = 74.74$; d.f. = 1; $P < 0.001$; Fig. 2b) in the presence of female mosquitofish (10.0%; 95% CI: 3.4–29.3%), than in the presence of male mosquitofish (73.3%; 95% CI: 59.1–91.0%). The average depth/gape ratio for tui chub larval prey consumed by female mosquitofish (0.72 ± 0.04; $N = 27$) was significantly <1.0 ($t = -6.5$; d.f. = 26; $P = 6.84$ e-7). The average depth/gape ratio of tui

chub larvae that survived in the presence of female mosquitofish was 0.91 (± 0.09), but not tested because of the small sample size ($N = 3$). The average depth/gape ratio for the tui chub larvae that survived with male mosquitofish predators (1.22 ± 0.06; $N = 22$) was significantly higher than 1.0 ($t = 3.58$; d.f. = 21; $P = 0.0018$). The depth/gape ratio of the tui chub larvae consumed by male mosquitofish was 1.06 (± 0.13), but not tested because of small sample size ($N = 3$).

Vulnerability modelling

Vulnerability modelling revealed that mosquitofish with a body depth <4.6 mm were completely vulnerable ($V = 1$) to tui chub predation. This corresponds to total lengths of 25.4 and 23.3 mm for female and male mosquitofish, respectively (females: total length = (body depth + 3.0746)/0.3017; $r^2 = 0.85$, $N = 90$, males: total length = (body depth + 0.8527)/ 0.2338; $r^2 = 0.78$, $N = 59$). However, with increasing size, vulnerability of mosquitofish to tui chub predation decreased to zero ($V = 0$) with a body depth > 12.8 mm (total length, female = 52.6 mm; Fig. 3a). The body depth of male mosquitofish never
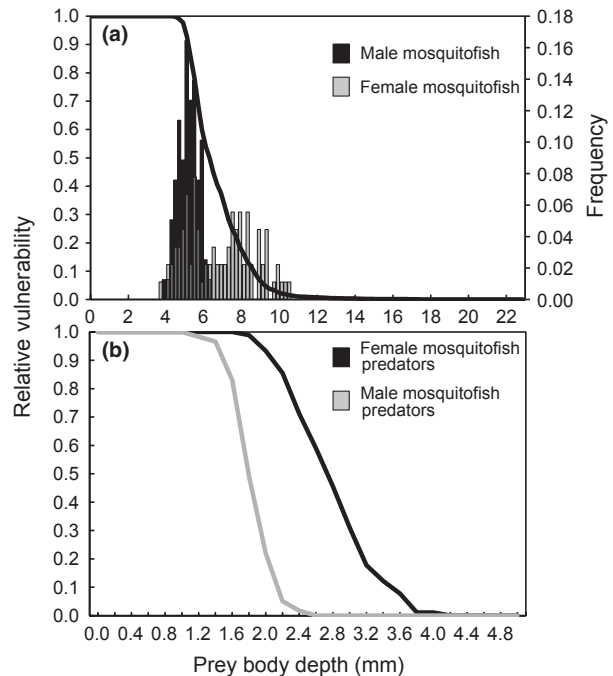

Fig. 3. Relative vulnerability (lines) of (a) mosquitofish (*Gambusia affinis*) prey under adult Mohave tui chub (*Siphateles bicolor mohavensis*) predation and (b) Mohave tui chub larval prey under adult mosquitofish predation. Frequency distribution of body depths of mosquitofish (a) are indicated with vertical bars and were constructed based on both male ($N = 59$) and female ($N = 90$) mosquitofish collected from Lake Tuendae in March–May 2009. The dark grey bars represent the portion of female mosquitofish size distribution overlapping with male mosquitofish size distribution.

reaches 12.8 mm, indicating that the entire Lake Tuendae male mosquitofish population is vulnerable to tui chub predation. Furthermore, the size distribution for the Lake Tuendae mosquitofish population shows that male mosquitofish have a higher vulnerability to tui chub predation compared to female mosquitofish because of relatively large body size of female mosquitofish (Fig. 3a).

Tui chub larvae with body depths <1.8 mm (total length = 11.2 mm) were completely vulnerable to predation by all size classes of adult female mosquitofish. With tui chub larval growth, their vulnerability to female mosquitofish predation decreases. The vulnerability to predation reaches zero when tui chub larvae reach a body depth >4.2 mm (total length = 23.3 mm), providing a complete size refuge from female mosquitofish predation. Tui chub larvae with body depths <1.2 mm (total length = 8.2 mm) were completely vulnerable to male mosquitofish predation; however, vulnerability of tui chub larvae to predation by adult male mosquitofish reached zero at a body depth of 2.6 mm (total length = 15.2 mm; Fig. 3b).

Discussion

This study provided experimental evidence that IGP between invasive western mosquitofish and native Mohave tui chub is gape-size limited. Correlated with their smaller size, male mosquitofish had higher vulnerability to tui chub predation than female mosquitofish. Similar results were obtained from two mesocosm experiments, where tui chubs caused low survival rates for male mosquitofish compared to female mosquitofish (Stockwell & Henkanaththegedara 2011; Henkanaththegedara 2012). Furthermore, gape-size limitation was indicated by the larger depth/gape ratio of surviving male mosquitofish compared to nonsurvivors.

The differential predation by male and female mosquitofish on tui chub larvae was also consistent with the gape-size limitation hypothesis. Adult female mosquitofish reduced tui chub larval survival by 90%, whereas male mosquitofish only reduced tui chub larval survival by 27%. Two lines of evidence suggest that mosquitofish predation on tui chub larvae was gape-limited. First, tui chub larval survival was notably lower in the presence of female mosquitofish (larger gapes) than in the presence of male mosquitofish (smaller gapes). Second, the depth/gape ratio was significantly smaller than 1.0 for tui chub larvae consumed by female mosquitofish, whereas the few survivors all had relatively larger body depths. The gape-size limitation of mosquitofish predation on larvae of native minnows was also reported where mosquitofish co-occur with native

least chub (*Iotichthys phlegethontis*). The survival of large young-of-the-year (YOY) least chub was greater than that of smaller YOY least chub (Mills et al. 2004).

Vulnerability modelling showed that gape-size limitation is likely to have important differential effects on survival of male mosquitofish at Lake Tuendae. Overall, the size frequency distribution of mosquitofish from Lake Tuendae suggests that all mosquitofish have some vulnerability to tui chub predation. However, male mosquitofish are more vulnerable to predation because of their relatively smaller body sizes compared to female mosquitofish. Vulnerability modelling also showed that all newly hatched tui chub larvae (total length = 6.56 ± 0.04 mm; $N = 30$) are completely vulnerable to both adult male and female mosquitofish predation. However, tui chub larvae may reach a complete size refuge from male and female mosquitofish as they grow.

The vulnerability model proposed by Hambright et al. (1991) is exceptionally liberal, because it assumes complete vulnerability to predation, if prey body depth is less that predator gape-size, that is depth/gape ratios ≤ 1.0. In our experiments, depth/gape ratio for consumed prey ranged from 0.7 (mosquitofish predators) to 0.9 (tui chub predators), which would reduce proportion of population vulnerable to predation (also see Truemper & Lauer 2005).

Collectively, our previous experiments (Stockwell & Henkanaththegedara 2011; Henkanaththegedara 2012) and the work described here provide evidence for gape-limited intraguild predation for this study system. Size-structured IGP has been suggested as an important mechanism, allowing co-existence of various interacting predatory communities (Polis et al. 1989), and may be an important mechanism, facilitating co-existence of Mohave tui chub and western mosquitofish. However, it is important to consider other mechanisms that may facilitate co-existence of these two species. For example, spatial and temporal niche segregation could also facilitate co-existence (see McHugh et al. 2012) of tui chubs and mosquitofish, but it appears that there is considerable overlap in habitat use. Larval tui chubs occupy the shallow areas of Lake Tuendae where mosquitofish abundance is high, making tui chub larvae vulnerable to mosquitofish predation (S.M. Henkanaththegedara, personal observations). Further, adult tui chubs forage very actively in the shallow areas at night (S.M. Henkanaththegedara, personal observations), making mosquitofish vulnerable to adult tui chub predation.

In addition to gape-size limitation, other aspects of predator–prey interactions such as adaptations of predators and antipredator behaviour of prey may play a role in IGP between tui chubs and mosquitofish. For

example, weak swimming ability of tui chub larvae (S.M. Henkanaththegedara, personal observations) may increase the vulnerability of tui chub larvae to mosquitofish predation. Additionally in the wild, factors that affect the detection distance of prey such as larval size, visual contrast and water clarity (Vinyard & O'Brien 1976) may play important roles in mosquitofish predation on larval tui chubs. However with growth, tui chub larvae may escape mosquitofish predation because of deep bodies coupled with improved predator detection ability and swimming ability (see Folkvord & Hunter 1986).

This case of IGP could have important evolutionary implications for both species. Because mosquitofish predation on tui chub larvae is size selective, larvae with faster growth rates are expected to have a survival advantage over slow-growing conspecifics under gape-limited predation (Stearns 1992; Sogard 1997); thus, IGP could select for faster growth rates in Mohave tui chub larvae. This case of IGP may also have important evolutionary effects on mosquitofish. First, relatively higher vulnerability of male mosquitofish to tui chub predation could skew adult sex ratios of mosquitofish. Altered sex ratios may alter the strength of sexual selection (Ashman & Diefenderfer 2001; Wade et al. 2003). Second, higher vulnerabilities of male mosquitofish may have effects on life-history evolution. Unlike female mosquitofish, male mosquitofish have a determinate-like growth pattern (Hughes 1986), making them vulnerable to tui chub predation throughout their entire lifespan. Thus, the relatively higher predation pressure on

Table 3. Size-dependent impacts of western mosquitofish, *Gambusia affinis*, and eastern mosquitofish, *G. holbrooki* (indicated with †), on native fish species.

No.	Species impacted	Mosquitofish interaction(s) with native fish species*	Maximum body size (mm)	Approach	Reference
1	Dwarf livebearer† *Heterandria formosa*	Significant negative effect of population growth	36	ME	Lydeard & Belk (1993)
2	Dwarf livebearer† *H. formosa*	Size selective predation on small individuals	36	ME	Belk & Lydeard (1994)
3	White Sands pupfish *Cyprinodon tularosa*	Significant impact on population size and biomass	50	ME	Rogowski & Stockwell (2006)
4	Spanish toothcarps† *Aphanius iberus* and *Valencia hispanica*	Heavy predation on juveniles	52*	ME	Rincon et al. (2002)
5	Big Bend gambusia *Gambusia gagei*	Endangerment of local populations	54	FO	Minckley & Deacon (1968)
6	Pacific blue-eye† *Pseudomugil signifer*	Lack of recruitment and reduced growth of adults	56‡	ME	Howe et al. (1997)
7	Gila topminnow *Poeciliopsis occidentalis*	Rapid replacement from most of its native range	60	FO	Minckley & Deacon (1968)
8	Sonoran topminnow *P. occidentalis*	Replacement in native range possibly by predation on of juveniles	60	LE, FE	Meffe (1985)
9	Sonoran topminnow *P. o. sonorensis*	Population decline by presumed mosquitofish predation	60	FO, FS	Galat & Robertson (1992)
10	Least chub *Iotichthys phlegethontis*	Reduction of survival and growth rate of larva/juveniles by predation	64	FE	Mills et al. (2004)
11	Rainbowfish *Rhadinocentris ornatus*	Apparent displacement from native habitat	65‡	FO	Arthington (1984)
12	White River springfish *Crenichthys baileyi*	Population decline by presumed mosquitofish predation	90	FB, FS	Deacon et al. (1964)
13	Barrens topminnow *Fundulus julisia*	Reduced survival of larva/juveniles by predation, injury risk to adults	94	LE	Laha & Mattingly (2006)
14	Black mudfish *Neochanna diversus*	Predation of mudfish larvae **Overall co-existence may be due to spatial/ temporal habitat partitioning**	106*	LE, FO	Barrier & Hicks (1994)
15	Mohave tui chub *Siphateles bicolor mohavensis*	Predation of tui chub larvae **Tui chub predation on mosquitofish**	300*	ME, LE	S.M. Henkanaththegdara and C.A. Stockwell, unpublished data
16	Green sunfish *Lepomis cyanellus*	Predation of sunfish larvae **Sunfish predation on mosquitofish**	310	FE	Blaustein (1991)
17	Largemouth bass *Micropterus salmoides*	**Largemouth bass predation on mosquitofish**	970	FE	Nowlin et al. (2006)

*Specific maximum body size was extracted from the reference cited.
‡Pusey et al. (2004); other values according to Page & Burr (1991).
Bold font refers to cases where co-existence may be facilitated by factors such as intraguild predation and niche segregation.
Approach code: ME, mesocosm experiments; FO, field observations; LE, laboratory experiments; FE, field experiments; FS, field surveys.

adult male mosquitofish is expected to select for maturation at smaller sizes (Reznick et al. 1990, 1996). Because evolution can occur over very short time scales (years – decades; Reznick et al. 1990; Hendry & Kinnison 1999; Stockwell et al. 2003), IGP may have already led to such contemporary evolution (*sensu* Hendry & Kinnison 1999) within this study system.

Our findings provide an important caveat to the dogmatic view of mosquitofish as a threat whenever they invade. Mosquitofish predation on eggs and/or larvae of native fish has been widely reported as a major threat to the existence of native fish (Meffe 1985; Mills et al. 2004; Rogowski & Stockwell 2006; Pyke 2008). However, it is important to note that many previous studies involved native species with relatively small body sizes, compared to the size of mosquitofish. To further evaluate whether mosquitofish impacts are limited to fishes with relatively smaller body sizes, we conducted a literature review. We searched Web of Science and Google scholar using the following keywords: mosquitofish, *Gambusia*, impacts and native fish (Table 3).

In 13 of 17 case studies, mosquitofish had negative impacts on small bodied native fish species (generally <65 mm; Table 3). By contrast, the remaining four studies included larger bodied fish species and showed co-existence of both species presumably because of reciprocal predation (Blaustein 1991; this study) or habitat partitioning (Barrier & Hicks 1994) despite mosquitofish predation on larvae or eggs of the native species. For example, mosquitofish co-existed with black mudfish (*Neochanna diversus*; grow up to 110 mm), despite mosquitofish predation on black mudfish larvae (Barrier & Hicks 1994; Ling 2004).

As for other systems (Polis et al. 1989; Arim & Marquet 2004), size-structured IGP appears to facilitate co-existence of endangered Mohave tui chub and invasive western mosquitofish. In fact, Mohave tui chub have co-existed with western mosquitofish for at least 9 years at Lake Tuendae (S. Parmenter, personal communication) and 27 years at China Lake (U.S. Fish & Wildlife Service 1984). Overall, our results suggest that a better understanding of trophic interactions may shed light on the mechanism(s) that facilitate the existence of native species in the presence of invasive species. This may lead to novel insights into species invasion and management options for invasive species.

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