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Foraging behaviour and invasiveness: do invasive *Gambusia* exhibit higher feeding rates and broader diets than their noninvasive relatives?

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Abstract – Serious impacts by nonindigenous species often occur via predation. The magnitude of impact is expected to be closely tied to the invading species niche breadth. For predatory impacts, diet breadth should be particularly important. We examined the relationship between a species foraging behaviour and its invasiveness and impact by comparing the feeding behaviour of four *Gambusia* species, two invasive and of high impact and two noninvasive. Individual feeding rates, feeding preferences, and diet breadths were tested across three prey items in a sequence of four laboratory feeding trials. Invasive *Gambusia* consistently fed at higher rates, but no species differences were found in feeding preferences or diet breadth. All *Gambusia* preferred *Daphnia*, avoided *Lirceus*, and consumed *Drosophila* in proportion to their availability. Female size affected most feeding variables. Larger fish consumed more prey per unit time and were able to incorporate larger prey items into their diets, thus increasing diet breadth.

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Predation is a major force shaping natural communities, affecting species abundances, distributions and composition (Paine 1966; Connell 1975; Sih et al. 1985; Power 1992). The structuring role of predation is particularly evident when predators are introduced outside their native range (Thorp 1986). Although only a small minority of nonindigenous species significantly affect invaded biotas (Simberloff 1981; Williamson 1996), when deleterious impacts occur, they often involve predation (Lodge 1993a). In particular, predation has been implicated as a major mechanism for species extinctions in invaded communities (Simberloff 1981; Moyle & Light 1996a; Mooney & Cleland 2001).

In aquatic systems, top predators have been shown to exert the greatest negative impact on invaded communities (Courtenay & Moyle 1992). The best-known example involves the introduction of the Nile perch *Lates niloticus* to Lake Victoria, which resulted in the extinction of over 200 of the 400 native haplochromine cichlids (Ogutu-Ohwayo 1999). In the United States, introductions of predatory centrarchids to western states have decimated native fish species already impacted by habitat alteration (Moyle 1976; Minckley 1991). In the Great Lakes, predation by introduced lamprey, alewife and rainbow smelt has dramatically altered fish assemblages (Moyle 1986) facilitating further invasion of the ecosystem (presently more than 140 nonindigenous species) (Mills et al. 1993).

Serious predatory impacts, however, not only result from large piscivorous species, but also from smaller omnivorous fishes (Moyle & Light 1996b). Predation by introduced mosquitofish, *Gambusia affinis* and *Gambusia holbrooki*, has been implicated in the extirpation of native fishes, amphibians and invertebrates

(Myers 1965; Schoenherr 1981; Meffe 1985; Courtenay & Meffe 1989; Lloyd 1989; Gamradt & Kats 1996; Howe et al. 1997; Goodsell & Kats 1999). Mosquitofish are aggressive foragers, feeding on a variety of prey, including the eggs, fry and larvae of native biota (Goodell et al. 2000). This is presumably the reason why they were widely introduced as a biocontrol agent against mosquitoes (and mosquito-borne diseases) in the early and mid- 1900s (Krumholz 1948). Presently, they are considered among the 100 worst invasive species worldwide (Lowe et al. 2000). In this study, we examined the foraging behaviour of these two highly invasive species in an effort to better understand the mechanisms underlying their high invasion success and impact.

The impact that invaders have on invaded communities should be intimately related to the invaders' niche breadth (Shea & Chesson 2002). Invading species with wider ecological niches will likely interact with a greater number of species (Goodell et al. 2000). For impacts via predation, diet breadth should be of particular interest. Diet generalists should have greater impacts than specialists (Ehrlich 1986; Ebenhard 1988; but see Bøhn & Amundsen 2001) and greater overall invasion success as prey resources may be rarely limiting (Moyle & Light 1996b). To explore how diet breadth and feeding behaviour in general, relate to invasiveness and impact, we compared feeding rates, feeding preferences and diet breadths of the highly invasive (and high impact) mosquitofish species to two noninvasive congeners. Comparisons of closely related species are an insightful approach to the identification of key traits conferring invasiveness (Mack 1996; e.g., Rejmanek & Richardson 1996). Two *Gambusia* species of relatively low invasive potential, *G. geiseri* and *G. hispaniolae*, were chosen for comparison. We hypothesized that *G. affinis* and *G. holbrooki* should exhibit both greater feeding rates and greater diet breadth (i.e. less diet preference) than *G. geiseri* and *G. hispaniolae*.

Methods

We quantified the feeding behaviour of 12 females of each *Gambusia* species in a sequence of four individual feeding trials. In the first three trials, maximum feeding rates on three different live prey items were quantified (one prey type per trial). In the fourth trial, the three prey items (in the same quantities as in first three trials) were offered to females simultaneously and total maximum feeding rates, feeding preferences and diet breadths were measured.

Females used in the experiment consisted of wild, gravid adults collected from within each species native range in the summer and fall of 1999. In

Gambusia, males typically reduce foraging and growth when sexually mature (Krumholz 1948) and may have a more specialized diet than females (Crivelli & Boy 1987; Blanco et al. 2004). Thus, females have a greater potential to impact prey communities. Adult females are also the gender and age class of interest in an invasion context. Female *Gambusia* are multiple-inseminated and able to store sperm for long periods of time (Zane et al. 1999), which allows them to start populations on their own without negative founder effects (Chesser et al. 1984). *Gambusia geiseri* and *G. affinis* females were collected from Comal springs and the Comal river, respectively, in Comal County, TX. *Gambusia holbrooki* females were collected from Leon Hines Lake, Escambia County, AL, and *G. hispaniolae* females were collected from La Azufrada spring, Lake Enriquillo, Dominican Republic.

The prey chosen for the study differed in microhabitat use and size; therefore, we maintained prey biomass constant (approximately 0.020 g) and varied prey number. In each trial, we used 40 *Daphnia pulex* (planktonic, 2.0 mm approximate length), 20 flightless *Drosophila melanogaster* (neustonic, 3.5 mm approximate length), and 15 isopods *Lirceus fontinalis* (benthic, 4.0 mm approximate length). *Daphnia* were collected from pond cultures at the University of Kentucky Ecological Research Facility, Lexington, KY, and *Lirceus* isopods were collected from Glenns Creek, Woodford County, KY. *Drosophila* were obtained from laboratory colonies also at the University of Kentucky.

Feeding trials were conducted in 6 l plastic tanks in two 9-day blocks (24 fish per block) in December 1999 and January 2000. Once isolated from stock tanks, females were given 48 h (days 1 and 2) to acclimate to individual tanks and were fed Tetramin® flakes (Tetra Werke, Melle, Germany) *ad libitum*. Prior to the experiment, females were not fed the experimental prey; instead, females consumed flakes and brine shrimp nauplii *ad libitum*. On days 3, 5 and 7, we conducted feeding trials with each single prey type. The order of the trials was randomized, so that for each species, two females experienced each of the six possible sequences. To standardize hunger levels, we conducted *ad libitum* feedings in between trials (days 4, 6 and 8) followed by a starvation period. Fish were allowed to consume flakes for 30 min, and then flakes were removed (23.5 h prior to next trial). On day 9, we conducted preference trials with all prey combined. No refuges or substrate were provided for either the prey or the *Gambusia*. For the duration of the experiment, water temperatures were maintained at 22.5 °C (±0.77) and photoperiod was kept constant at 14 h light:10 h dark. Periodic water changes (50% of volume) were conducted to maintain water quality

instead of using aeration or filters that might interfere with prey or *Gambusia* foraging behaviour.

Trials ran for either 10 min or until all prey were consumed. From observations conducted during trials, we calculated maximum feeding rates (number of prey consumed divided by trial duration). To quantify feeding preferences in the fourth trial, we computed selection indices w_i for each prey item (Manly et al. 1993):

$$w_i = \frac{c_i}{a_i} \qquad (1)$$

where c_i is the proportion of prey i consumed and a_i is the proportion of prey i available. Selection indices were then standardized (so that they add up to 1.0) by dividing each selection index by the sum of the three indices:

$$S_i = \frac{w_i}{\sum w_i} \qquad (2)$$

As three prey were available to *Gambusia*, selection indices above 0.33 indicate relative preference, whereas values below 0.33 indicate relative avoidance. To assess diet breadth, we then calculated Hurlbert's (1978) measure of niche breadth, N:

$$N = \frac{1}{\sum (c_i^2 / a_i)} \qquad (3)$$

where c_i and a_i are as defined above. Diet breadth was also standardized using the following equation:

$$B = \frac{N - a_{\min}}{1 - a_{\min}} \qquad (4)$$

where $a_{\min}$ is the smallest proportion of prey available.

Statistical analyses

A repeated measures ANCOVA with female size (standard length) as a covariate was used to test for a species effect on the four feeding rates. Species differences on the feeding preference and diet breadth measures were tested with a MANOVA followed by ANOVAS or ANCOVAS if female size was a significant covariate. Female size distributions overlapped among the four species (Figs 1 and 2). Mean female size was intermediate for the invasive species (30.0 cm for *G. holbrooki*, and 35.0 cm for *G. affinis*), largest for *G. hispaniolae* (36.7 cm) and smallest for *G. geiseri* (27.4 cm). To meet parametric test assumptions, feeding rates were log-transformed (Ln of observed value + 1) and selection indices and diet breadths were arcsin square-root transformed prior to analysis.

T-tests were used to test whether mean selection indices for each *Gambusia* species differed from 0.33 (the no-preference value). Simple linear regressions were used to test the nature of the relationship between female size and the foraging variables if size was a significant covariate. Preliminary analyses indicated no effect of prey sequence or the time blocking factor
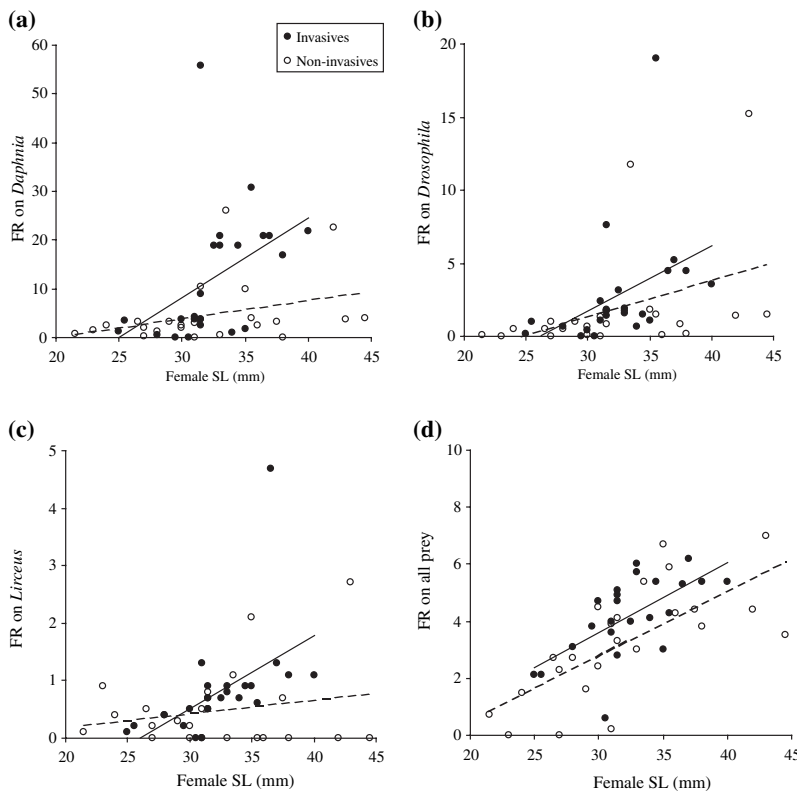

Fig. 1. Feeding rates (FR) in numbers of prey consumed per minute of trial time on (a) *Daphnia*, (b) *Drosophila*, (c) *Lirceus* and (d) on all three prey combined as a function of female standard length (SL) in cm. Separate least-squares regression functions were fitted to the invasive *G. affinis* and *G. holbrooki* (solid lines; *Daphnia*: $r^2 = 0.34$, $P = 0.003$, *Drosophila*: $r^2 = 0.36$, $P = 0.002$, *Lirceus*: $r^2 = 0.41$, $P = 0.001$, and all prey: $r^2 = 0.33$, $P = 0.004$) and the noninvasive *G. geiseri* and *G. hispaniolae* (dashed lines; *Daphnia*: $r^2 = 0.14$, $P = 0.073$, *Drosophila*: $r^2 = 0.25$, $P = 0.01$, *Lirceus*: $r^2 = 0.01$, $P = 0.24$, and all prey: $r^2 = 0.0001$, $P = 0.45$).
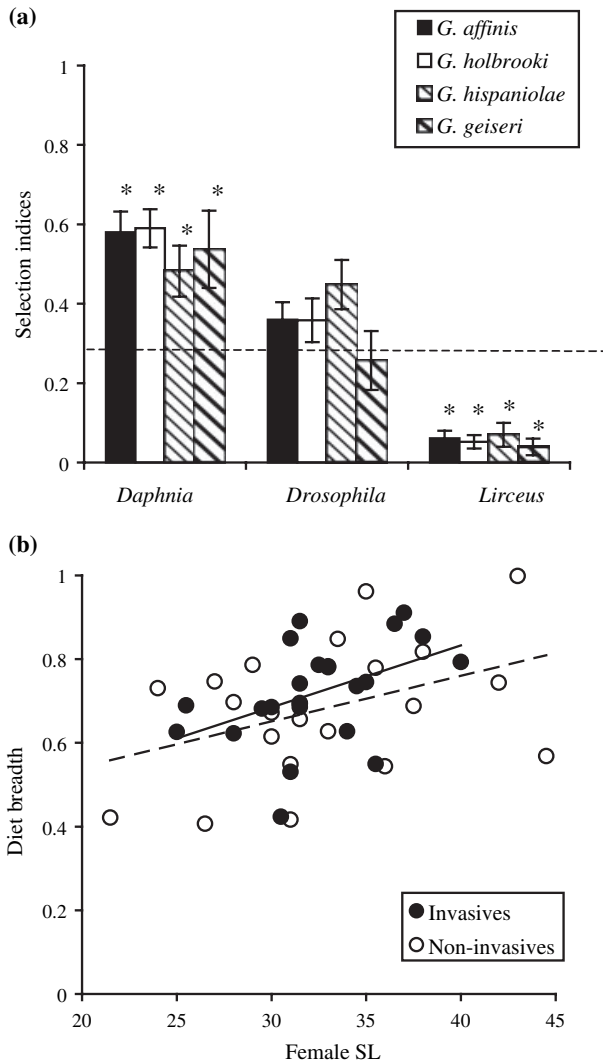
(a)

(b)

Fig. 2. (a) Prey selection indices (mean ± 1 SE) measured when all prey where offered simultaneously for each *Gambusia* species. The dotted line (0.33) indicates no preference. Asterisks denote significant differences from 0.33 at the $P = 0.05$ significance level. Plain bars denote the invasive *Gambusia* species, whereas striped bars denote the noninvasive species. (b) Hurlbert's measure of diet breadth plotted as a function of female SL (cm) for the invasive (solid least-squares regression line; $r^2 = 0.21$, $P = 0.028$) and noninvasive *Gambusia* (dashed least-squares regression line; $r^2 = 0.19$, $P = 0.04$).

on any of the variables; thus these effects were left out of final analyses reported here.

Orthogonal contrasts were used to test for species differences once a significant species effect was found. In three contrasts, we tested whether the two invasive species differed from the two noninvasive species (one-tailed test, we had the *a priori* hypothesis that invasive species should feed at a higher rate on all prey types than noninvasive species) and whether there were significant differences between species within the invasive category (*G. affinis* versus *G. holbrooki*, two-tailed test) and between species within the noninvasive

category (*G. geiseri* versus *G. hispaniolae*, two-tailed test). Bonferroni pairwise comparisons were used to compare the four feeding rates. All tests were conducted using SAS® Version 8.02.

Results

Feeding rates on individual prey were highest on *Daphnia*, lowest on *Lirceus*, and intermediate on *Drosophila* (Table 1; Fig. 1a–c). On average, *Gambusia* females consumed eight *Daphnia*, two *Drosophila*, and one *Lirceus* per minute of trial time (Bonferroni pairwise comparisons, all $P < 0.0001$). Feeding rates on all three prey combined during trial 4 were comparable with feeding rates on *Daphnia* alone, but higher that rates on the other two prey (all three prey combined versus *Daphnia*: $P = 0.198$, other comparisons: $P < 0.0001$). Feeding rates also varied among *Gambusia* species (Table 1). Orthogonal contrasts showed that feeding rates were consistently higher for invasive *Gambusia* than their noninvasive relatives ($F_{1,42} = 6.8$, $P = 0.012$). Feeding rates on *Daphnia* were two and a half times higher for the invasive females (Fig. 1a). Similarly, feeding rates on *Drosophila* and *Lirceus* were 50% and 70% higher respectively for invasives (Fig. 1b and c). Feeding rates when all three prey types were available were 30% higher for *G. affinis* and *G. holbrooki* compared with *G. geiseri* and *G. hispaniolae* (Fig. 1d). We detected no difference in feeding rates between the two invasive species (*G. holbrooki* versus *G. affinis*: $F_{1,42} = 0.04$, $P = 0.844$), nor between the two noninvasives (*G. geiseri* versus *G. hispaniolae*: $F_{1,42} = 1.2$, $P = 0.273$).

The MANOVA comparing the preference and diet breadth measures showed no species effect (Wilks' lambda, $F_{12,101} = 0.7$, $P = 0.75$) indicating that invasive and noninvasive *Gambusia* exhibited similar feeding preferences and diet breadth. Individual ANOVAS and ANCOVAS confirmed this result (species effects: *Daphnia*, $F_{3,40} = 0.4$, $P = 0.73$; *Drosophila*, $F_{3,41} = 1.0$, $P = 0.38$; and *Lirceus*, $F_{3,40} = 1.1$, $P = 0.38$). In general, all species preferred *Daphnia*, consumed *Drosophila* in proportion to their availability, and avoided *Lirceus* (Fig. 2a). For *Daphnia*,

Table 1. Summary of results from a repeated measures ANCOVA performed on feeding rates measured on the three individual prey items (*Daphnia*, *Drosophila* and *Lirceus* sp.) in trials 1–3, and on all prey combined during trial 4.

Effect	d.f.	F	P-value
Species	3, 42	2.9	0.047
Female size	1, 42	13.2	0.001
Feeding rates	3, 129	61.1	0.0001
Feeding rates × species	9, 129	1.5	0.16

selection indices of all *Gambusia* were consistently higher than 0.33 (*t*-tests; *G. affinis* and *G. holbrooki*: $P = 0.001$, *G. hispaniolae*: $P = 0.036$, and *G. geiseri*: $P = 0.003$), whereas for *Lirceus*, selection indices were consistently lower than 0.33 ($P = 0.0001$ for all species). Diet breadths also did not differ significantly among the species ($F_{3,40} = 0.6$, $P = 0.60$; Fig. 2b). Hurlbert' measure of diet breadth averaged 0.72 for *G. affinis* and *G. holbrooki* and 0.68 for *G. geiseri* and *G. hispaniolae* reflecting the fact that females consumed primarily two of the three prey items available (*Daphnia* and *Drosophila*) (Fig. 2a).

As may be expected, fish size affected most measures of foraging behaviour. Generally, larger *Gambusia* fed at higher rates, although the relationship between size and foraging rates seem to be more consistent in invasive *Gambusia*. All four invasive feeding rates were positively related to fish size; whereas for the noninvasives, only rates on *Drosophila* and all prey combined were significantly related to size (Fig. 1). When given a choice, larger fish also had broader diets (covariate in ANCOVA: $F_{1,40} = 8.0$, $P = 0.007$), although the relationship between size and diet breadth was not particularly strong ($r^2 = 0.18$, $P = 0.003$) (Fig. 2b). As female size increased, preference for *Lirceus*, the largest prey, increased (covariate in ANCOVA: $F_{1,40} = 8.3$, $P = 0.006$; regression: $r^2 = 0.10$, $P = 0.021$); and preference for *Daphnia*, the smallest prey, decreased (covariate in ANCOVA: $F_{1,40} = 8.0$, $P = 0.007$; regression: $r^2 = 0.18$, $P = 0.002$). Only larger *Gambusia* appeared able to incorporate the larger prey items into their diets, thus increasing their diet breadth.

Discussion

The foraging behaviour of predatory species is expected to be a key factor affecting their invasiveness and impact in invaded communities (Lodge 1993b). Species or organisms that are opportunistic foragers and diet generalists are typically expected to achieve greater invasion success and impact. However, few studies of foraging behaviour (and of behaviour in general) have tested this expectation (Holway & Suarez 1999). Furthermore, few invasion studies address these questions empirically (Parker & Reichard 1998; Williamson 1999) or comparatively (Vermeij 1996). In invasive *Gambusia*, research on foraging behaviour is clearly needed to better understand the impact of their introductions (Garcia-Berthou 1999). The results from this simple comparative study provide evidence that invasive *Gambusia* species might be superior foragers relative to noninvasive congeners. *Gambusia affinis* and *G. holbrooki* exhibited higher feeding rates on all prey tested compared with their noninvasive relatives, *G. geiseri* and

G. hispaniolae. In a previous study with the same prey, *G. affinis* and *G. holbrooki* also foraged more efficiently and consumed more prey than *G. geiseri* and *G. hispaniolae* (Rehage et al. 2005).

However, diet preference and breadth results contradict the classic notion that invasive species, especially those with significant predatory impact, should have broad diets (Ehrlich 1986; Lodge 1993b; Moyle & Light 1996a). Selection indices on the three prey used in the experiment and overall diet breadth were identical for invasive and noninvasive *Gambusia*. All *Gambusia* preferred *Daphnia*, the smallest prey item, exhibited no significant preference for *Drosophila*, and avoided *Lirceus*. It is plausible that this lack of variation among species is an artefact of the particular prey used or the small number of prey items included in the study. Alternatively, strong differences in prey profitability and density may have resulted in females of all species making similar foraging choices (see below). Future work should include preference assays with a greater variety of prey in conjunction with gut content and stable isotope analyses to better elucidate the link between diet breadth and mosquitofish invasiveness and predatory impact.

Whereas little is known about the foraging behaviour of noninvasive *Gambusia*, invasive mosquitofish are considered generalist predators (Farley 1980). The mosquitofish diet is typically composed of zooplankton, drifting and benthic invertebrates, and terrestrial and neustonic prey (Lloyd et al. 1986; Garcia-Berthou 1999). Mosquitofish are known to significantly alter aquatic communities because of their direct predatory effects on these organisms, particularly zooplankton (Hurlbert et al. 1972; Hurlbert & Mulla 1981; Harris 1995; Margaritora et al. 2001; Blanco et al. 2004). Stomach-content analyses show that crustaceans including daphniids often constitute a significant proportion of the diet (Hurlbert & Mulla 1981; Crivelli & Boy 1987; Blaustein & Karban 1990; Garcia-Berthou 1999). The higher feeding rates and strong preference for *Daphnia pulex* seen in fish in our experiment concur with these dietary observations.

Although, our study only examined the foraging behaviour of females, we expect that the higher foraging rates of invasives females are representative of other life stages, at least juveniles. Male mosquitofish significantly reduce foraging once mature (Krumholz 1948; Blanco et al. 2004), and we would expect the same to be true for other *Gambusia* species. Invasive juveniles may be expected to feed more voraciously than noninvasive juveniles, although not necessarily on the same prey items as adults. Diet overlap among life stages may be high, but during the reproductive season female diet has been shown to shift significantly (Crivelli & Boy 1987). Ontogenetic diet shifts have been documented in invasive

Gambusia; juveniles consume smaller prey such as diatoms, rotifers and copepod nauplii, and as adults may switch to larger prey, such as chironomids and cladocerans (Garcia-Berthou 1999; Blanco et al. 2004).

In invaded areas, mosquitofish feed opportunistically on naive prey that have no evolutionary history with mosquitofish predation. Naive prey, often eggs and larval stages of amphibians and fishes, either completely lack antipredator responses or show responses that are ineffective against novel predation by mosquitofish (e.g. Gamradt & Kats 1996). This trophic opportunism allows mosquitofish to decimate local prey populations and threatens the long-term persistence of many aquatic species in invaded communities (Meffe 1985; Courtenay & Meffe 1989; Arthington 1991). The higher foraging rates of invasive *Gambusia* across different prey noted in our trials are consistent with this opportunistic foraging style. Alternatively, these higher foraging rates may have resulted from a prior preference or experience with similar prey since we used wild females. It is also plausible that differences in energetic requirements stemming from their experiences in the wild may underlie this variation in foraging rates. Future studies examining foraging behaviour in this and other systems would benefit from removing potentially confounding effect of experience and condition by using laboratory-reared individuals the have been fed standardized diets.

Feeding preferences were highest for *Daphnia*, intermediate for *Drosophila*, and lowest for *Lirceus*. These results contradict the simple expectation that large prey should be preferred because of their higher energy content (Werner & Hall 1974). However, larger prey may not necessarily be more profitable. Prey profitability (energy per unit handling time) may decrease with increasing prey size if handling and/or digestion times become disproportionately large (Bence & Murdoch 1986; Kaiser et al. 1992; Sih & Christensen 2001). This may explain the strong preference for *Daphnia* in all four *Gambusia* species. *Daphnia* may have been in fact the most profitable prey, as handling times (although not directly quantified) seemed virtually instantaneous for *Daphnia*, but were relatively long for *Drosophila* and even longer for *Lirceus* (J. S. Rehage, personal observation). Previous studies on invasive *Gambusia* foraging behaviour have shown that these fish often preferentially consume small prey (Bence & Murdoch 1986; Arthington 1991; Garcia-Berthou 1999).

The strong preference for *Daphnia* may have also resulted from a prey density effect: *Gambusia* were attacking and consuming the most frequently detected prey. Encounter rates were most likely higher and search times lower for *Daphnia* relative to the other two prey species, not only because *Daphnia* were in the highest density, but also because *Daphnia* were in the water column whereas flies and isopods were limited to either the water surface or the tank bottom. These differences in prey distribution may have resulted in distinct prey patches, in which case prey density may matter. Although optimal foragers are typically expected to ignore density and choose prey according to profitability only (MacArthur & Pianka 1966), if prey are patchy, foragers should respond to density by spending more time in the most profitable patches (i.e. the water column) where prey are aggregated (Hassell & May 1974). Regardless of the mechanism and contrary to our predictions, invasive and noninvasive *Gambusia* seemed to be making identical foraging choices, and thus exhibiting very similar diet preferences and equal diet breadths, at least at the scale of this experiment.

Although size distributions were similar among invasive and noninvasive *Gambusia* (and mean sizes were intermediate for invasives), female size affected all foraging variables. The effect was similar for the invasive and noninvasive species. Larger fish of both species types consumed more prey per unit time and were able to include larger prey items into their diet, increasing diet breadth. This result may have important implications for *Gambusia* impact in light of recent research documenting body size changes in invaded communities. Several studies have reported greater body sizes for invaders in their invaded range relative to their native range (Crawley 1987; Willis & Blossey 1999; Grosholz & Ruiz 2003; Leger & Rice 2003), presumably a response to a release from natural enemies in the introduced range (Keane & Crawley 2002). Introduced *Gambusia* have been shown to have lower loads of parasites than either ecologically similar native fishes in the invaded range or their native populations (Dove 2000). This enemy release could allow *Gambusia* to achieve greater sizes in invaded areas; and according to our results, these larger fish will also have higher feeding rates and diet breadth, and the potential for greater impact.

A few studies have examined whether diet or diet breadth is a key correlate of invasion success and impact. Among them, studies on birds introduced to oceanic inlands provide some of the best evidence on the relationship between species-specific traits and invasion success given that detailed records exist on both failed and successful introductions (Kolar & Lodge 2001). In such studies, the relevance of diet as a predictor of invasion success has mixed support. McLain et al. (1999) reported diet to be a significant predictor (among other traits) of introduction success for 132 bird species brought to nine oceanic islands. Bird species that incorporated both seeds and fruit into their diets were more likely to establish than more

restricted foragers. Duncan et al. (2001) found that omnivorous and carnivorous diets were good predictors of establishment success for birds introduced to Australia but were unrelated to the amount of spread of these species. Diet breath was not correlated with establishment in birds introduced to New Zealand (Veltman et al. 1996).

Among fishes, evidence on the significance of diet breadth as an important ecological trait conferring invasiveness is also conflicting. Marchetti et al. (2004) showed that for nonindigenous fishes in California, diet breadth was not a good predictor of establishment but was positively correlated with spread and abundance (surrogates for impact) in invaded watersheds. Kolar & Lodge (2002) found that neither the establishment, spread, nor impact of nonindigenous fishes in the Great Lakes region was predicted by diet breadth. These studies seem to indicate that the predictive power of diet breadth in the context of invasion success and impact might be limited. This may be especially true when we compare diet breadth to life-history characters (Sakai et al. 2001) and characteristics of the invasion effort (i.e. propagule pressure) (Williamson 1999), which seem to consistently correlate with measures of invasion success. Future studies on the foraging behaviour of invasive species might focus not just on diet breadth, but on other aspects of foraging, such as voracity *per se* and other measures of foraging plasticity (e.g. foraging innovations; Sol et al. 2002).

Resumen

1. Los efectos negativos causados por especies introducidas e invasoras generalmente ocurren a través de la predacion. Para estas especies, la magnitud de sus efectos esta íntimamente relacionada con características de su comportamiento de forrajeo y dieta. En esta investigación, comparamos el comportamiento de forrajeo de dos especies de peces invasoras y de gran impacto en comunidades acuáticas invadidas, *Gambusia affinis* y *Gambusia holbrooki*, a dos especies muy relacionadas pero no invasoras, *G. geiseri* y *G. hispaniolae*. Comparar especies muy relacionadas es un método útil para detectar su habilidad para invadir nuevas comunidades.

2. En tres experimentos, cuantificamos tasas de alimentación máximas en tres presas diferentes, *Daphnia pulex*, *Drosophila melanogaster* y *Lirceus fontinalis*, ofrecidas individualmente a hembras de cada especie de *Gambusia*. En un cuarto experimento, las tres presas fueron ofrecidas a la vez, sobre las que calculamos las tasas de alimentación totales, preferencias dietéticas y amplitud de dietas de las especies de *Gambusia*.

3. Las especies invasoras *G. affinis* y *G. holbrooki* consumieron las tres presas (ofrecidas individualmente o juntas) en tasas consistentemente mas altas que *G. geiseri* y *G. hispaniolae*. En contra de nuestra expectativa, no encontramos diferencias ni en los índices de preferencia ni en la amplitud de dieta entre las especies invasoras y no invasoras. Las cuatro especies de *Gambusia* demostraron preferencia por las presas más pequeñas

i.e., *Daphnia*, consumieron *Drosophila* en proporción a su existencia y evitaron consumir las presas mas grandes i.e. *Lirceus*. El tamaño de las hembras afectó a la mayoría de las variables medidas en nuestro estudio. Los individuos mayores de *Gambusia* demostraron tasas de alimentación más altas y consumieron presas más grandes, incrementando así la amplitud de sus dietas.

Acknowledgements

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