

# Enhanced interspecific territoriality and the invasion success of the spotted tilapia (*Tilapia mariae*) in South Florida

Wesley R. Brooks · Rebecca C. Jordan

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**Abstract** South Florida's freshwaters are amongst the most invaded in the world with 34 naturalized fish species. How these non-natives affect the local native fish populations, however, is largely unknown. Native sunfish of the genus *Lepomis* are important as predators in structuring fish and invertebrate assemblages in the swamps and seasonal wet prairies of the Big Cypress Swamp and Florida Everglades. The spotted tilapia, *Tilapia mariae*, is a successful West African invader that exhibits territorial and spawning behavior that closely matches that of native *Lepomis* sunfishes. We tested the hypothesis that *Lepomis* sunfishes and *T. mariae* would compete when space was limiting. Additionally, we predicted that *T. mariae*, because of their aggressiveness, would be more successful in acquiring space. We collected juveniles of both groups from Big Cypress National Preserve, Everglades National Park, and the South Florida Water Management District canal system for laboratory trials in which likely competitive interactions were staged and observed. *T. mariae* were bolder and more aggressive than *Lepomis* sunfishes. *T. mariae* residents resisted all intruders whereas 30% of *Lepomis* sunfish residents were ejected. We surmise that these enhanced

behaviors of *T. mariae* are an important component of their success in South Florida. The continued spread of *T. mariae* populations throughout South Florida into natural habitats suggests an increasing potential to affect the quality of spawning habitat available for *Lepomis* sunfishes and warrants a renewed focus on *T. mariae* as a non-native species of special concern.

**Keywords** Big cypress swamp · Competitive interactions · Fish invasions · Florida Everglades · Interspecific competition · *Lepomis* sunfish · South Florida · Spotted tilapia · Territorial behavior

## Introduction

South Florida has experienced a high rate of non-native freshwater fish introductions since the 1960's (Courtenay and Robins 1975; Shafland 1996a, b), with 34 species categorized as having self-sustaining populations (Shafland et al. 2008). This is likely due in part to low species richness of the native fish community (Moyle and Light 1996; Gido and Brown 1999), as well as vast anthropogenic alterations of the region's hydrology and aquatic habitats (Moyle and Light 1996; Marchetti et al. 2004). Attempts to prevent such introductions and manage non-native populations that become naturalized are often limited by insufficient biological knowledge and a lack of environmental and economic impact data (Simberloff et al. 2005). While evidence for deleterious ecological effects of

W. R. Brooks (✉) · R. C. Jordan  
Department of Ecology, Evolution and Natural Resources,  
Rutgers University, 14 College Farm Rd, ENR Bldg,  
School of Environmental and Biological Sciences,  
New Brunswick, NJ 08901, USA  
e-mail: wrbrooks@rci.rutgers.edu

non-native fishes on native aquatic communities has been documented in many watersheds (Taylor et al. 1984), there are no experimental data from South Florida that demonstrate strong negative interactions by non-native fishes on native fish populations or communities (Shafland 1996b; Courtenay 1997; Fuller et al. 1999; Trexler et al. 2000). A few qualitative assessments of the region's fish communities have reported localized shifts in species composition and abundance following the establishment of non-native fishes (Courtenay and Hensley 1979; Kushlan 1986; Loftus and Kushlan 1987). These reports, however, are speculative in nature and likely are more indicative of fish communities in the urban canals of Southeast Florida (see Shafland 1999) as opposed to communities in natural wetlands (Trexler et al. 2000).

The Spotted Tilapia, *Tilapia mariae*, has received particular attention in South Florida as a non-native fish of high concern (Shafland 1976; Courtenay and Hensley 1979). Native to lowland rivers of tropical West Africa (Ikomi and Jessa 2003), this algivore/detritivore was likely introduced through escape from aquaculture into Miami's urban canal system in the early 1970's (Hogg 1974). Within a few years of introduction, *T. mariae* replaced another introduced cichlid, the Black Acara (*Cichlasoma bimaculatus*), as the most abundant fish by biomass in urban canals (Courtenay and Hensley 1979). *T. mariae* has expanded its range via the canal system throughout South Florida and is now routinely captured in other artificial wetlands including restoration marshes, rice fields, agricultural ditches (Chimney and Jordan 2008), as well as natural wetlands in the Everglades and Big Cypress regions including freshwater marsh (Chick et al. 2004), wet prairie (Trexler et al. 2000; Chick et al. 2004), slough (Chick et al. 2004), and cypress swamp habitats (Chimney and Jordan 2008). In Everglades National Park, where it has most recently invaded, *T. mariae* already constitutes 4.5 and 3.1%, respectively, of the abundance of the large fish catch in Shark River and Taylor sloughs, and has replaced the Mayan Cichlid, *Cichlasoma urophthalmus*, as the most abundant non-native species in the former (Chick et al. 2004).

Courtenay and Hensley (1979) suggested that *T. mariae* was likely to impact native fishes, especially *Lepomis* sunfishes and other Centrarchids, through competition for space and spawning habitat. Like *T. mariae*, the *Lepomis* sunfishes including the Warmouth (*L. gulosus*), Bluegill (*L. macrochirus*),

and Spotted Sunfish (*L. punctatus*) are territorial substrate spawners (Loftus and Kushlan 1987). Additionally, *T. mariae* and *Lepomis* sunfishes overlap in spawning season (Loftus and Kushlan 1987), and have been observed nesting in close proximity to each other, interacting via displays and chases (Hogg 1974; Annett et al. 1999; Trexler et al. 2000). This suggests a strong potential for territorial competition that, to date, has not been empirically tested.

*T. mariae* individuals are aggressive and territorial towards conspecifics and interspecifics throughout their native range (King and Etim 2004). Interspecific aggression and territoriality by non-natives can contribute to invasion success (Holway and Suarez 1999; Moyle and Marchetti 2006), and lead to the displacement of natives from preferred microhabitats such as spawning sites (Taylor et al. 1984). These spatial alterations can impact individual growth rates and population densities leading to a host of direct and indirect ecological effects in the native community (Taylor et al. 1984). Moreover, habitat structure can play an important role in determining competition intensity between native and non-native competitors (Petren and Case 1998). Specifically, habitat structure may affect the effort that one or both competitors will invest in the acquisition or defense of a territory (Johnsson et al. 2000). Consequently, the scope of the potential impacts of *T. mariae* on *Lepomis* sunfishes might be limited to certain habitats and not applicable across all of their shared range.

We directly tested the notion that non-native *T. mariae* and native *Lepomis* sunfishes will actively compete for space. More specifically, we tested the hypothesis that individuals of *T. mariae* would be more aggressive towards interspecifics than their *Lepomis* sunfish competitors resulting in enhanced territorial acquisition and defense. We also expected that different habitat structures might have a significant effect on the potential outcomes of competitive interactions, with one or both groups exhibiting modified behavior in each habitat type.

## Methods

### Collection and housing

Juvenile *Lepomis* sunfishes (*L. gulosus*, *L. macrochirus mysticallis*, and *L. punctatus punctatus*) and

*T. mariae* cichlids, measuring 3–6 cm total length (TL) were collected from fifteen sites throughout South Florida within a range of urban and natural areas (Fig. 1). Fish were transferred to New Jersey and conditioned to the laboratory environment. In the laboratory, individuals were maintained in same-species 110-l tanks maintained at 24–28°C, pH 7–8, and 12-h broad-spectrum light/dark cycle. The fish were fed a combination of flake and stick foods three times daily. Except for feeding, occasional care, and tank maintenance, the fish were not disturbed during the 3 months prior to experimentation.

Experimental tanks were 18 liters in volume with a bottom surface area of 0.1 m<sup>2</sup>. The tank bottoms were covered in sand to a depth of 2 cm and outfitted with a power filter to oxygenate and clean tank water. All individuals used were pre-reproductive and unsexed with a mean standard length (SL) during trials of 4.9 cm (smallest individual- 3.8 cm; largest individual- 6.2 cm).

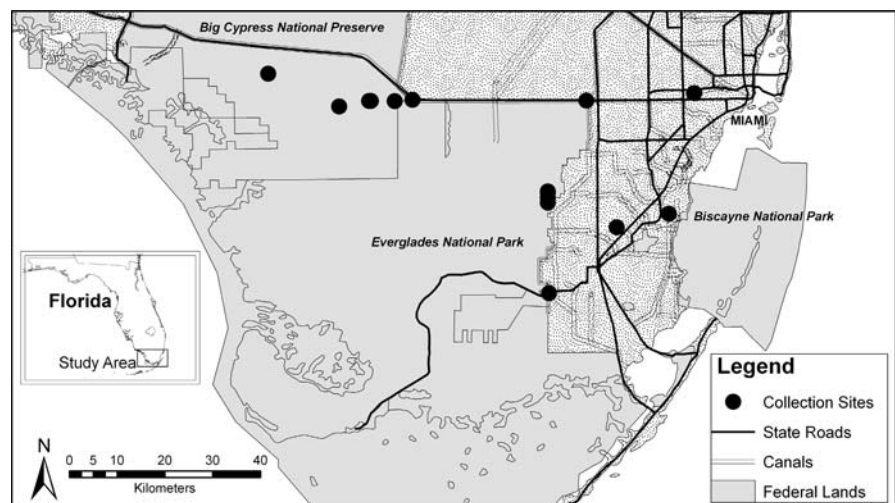
### Residency trials

The focus of each residency trial was to monitor the behavioral interactions between the resident and a size-matched (within 10% total length) intruder over the first 15 min of their cohabitation. Twenty *T. mariae* (TM) and twenty *Lepomis* sunfishes (12 *L. gulosus* (LG), 4 *L. macrochirus* (LM), 4 *L. punctatus* (LP)) were randomly selected, measured, and isolated individually in experimental tanks. These ‘residents’ were allowed to acclimate for 3 days prior

to experimentation in order to establish residency. The remaining pool of unused individuals were designated as ‘intruders’ and were maintained in small same-species groups to facilitate easier individual identification and capture for measurement and trial usage. Residents were used in each of four consecutive trials which varied in terms of competition type (Interspecific: TM versus LG/LM/LP, Intraspecific) and habitat structure of the tank (microhabitat 1: sandy bottom only, microhabitat 2: sandy bottom with small PVC tube, microhabitat 3: sandy bottom with artificial plants blocking swimming in the top half of the tank). Intraspecific trials were performed in order to provide a baseline for behavioral data for both *T. mariae* and the three *Lepomis* sunfish species utilized in this study. It should be noted that it was necessary to use nine intruders (five LG, one LP, three TM) twice during residency trials; however, the same resident-intruder pairing was never repeated to avoid confounding and pseudoreplication.

A series of four 15-min video-recorded trials were conducted per resident, with the intruders removed promptly after each trial. All fish were given a full day of rest between trials, allowing residents to familiarize themselves with new habitat structures. The four trials were conducted in the following sequence per resident: (1) intraspecific encounter in microhabitat 1, (2) interspecific encounter in microhabitat 1, (3) interspecific encounter in microhabitat 2, (4) interspecific encounter in microhabitat 3. In all, 160 residency trials were conducted; 80 trials featuring TM residents (of these there were 20 intraspecific

**Fig. 1** Map of South Florida collection sites



pairings, 36 TM-LG pairings, 15 TM-LM, and nine TM-LP pairings) and 80 trials featuring *Lepomis* sunfish residents (of these there were 12, four, and four intraspecific trials for LG, LM, and LP, respectively, 36 LG-TM pairings, and 12 LM-TM and LP-TM pairings each).

#### Scramble trials

Scramble trials consisted of inducing interspecific competition by simultaneously introducing one size-matched intruder of each group (*T. mariae* versus *Lepomis* sunfishes) to an empty experimental tank with microhabitat 1. Each trial was recorded on video for 15 min from the time of introduction, and both fishes were promptly separated and removed afterwards. In all, 20 scramble trials were conducted (of these ten were LG-TM pairings, and five each were LM-TM and LP-TM pairings).

#### Video analysis

Recorded trials were divided among three individuals, all of whom blindly evaluated a sample of videos in common in order to measure viewer congruency (over 80% agreement). Viewers measured the number of aggressive contacts inflicted on one another (aggression) and the time, in seconds, it took for each fish to log its first aggressive contact (boldness). In cases where an individual failed to inflict any aggressive contacts on a competitor, it was assigned a boldness score of 900 s (the equivalent of the full 15-min trial). Additionally, viewers were asked to evaluate the winner of each territorial contest (dominance) by observing signs of victory and defeat via fin positioning, attentiveness, and general attitude.

#### Statistical analysis

##### *Interspecific territorial competition*

To determine what factors, if any, predicted aggression and boldness in interspecific residency trials, we used two separate GLM ANOVAs with Residency Status (Resident, Intruder), Species (TM, LG, LM, LP), and Habitat (Microhabitat 1, Microhabitat 2, Microhabitat 3) as fully-fixed and fully-crossed factors for all interspecific trials (Minitab v.13.0).

The response variables for these GLM ANOVAs were each individual fish's corresponding square-root transformed aggression and boldness measures. Additionally, simultaneous Tukey's HSD tests were conducted on the models' significant main and interaction effects with a global  $\alpha$ -level set at .05 to discern the specific patterns of aggression and boldness in interspecific competition between *T. mariae* and *Lepomis* sunfishes. Finally, to evaluate our hypothesis that increased aggression in *T. mariae* resulted in improved territorial retention as compared to *Lepomis* sunfishes we tested the correlation between individual aggression and dominance.

##### *Intraspecific versus interspecific competition comparison*

To determine whether there were differences in the behavior of individuals with regard to the nature of the territorial competition (intra- versus interspecific) incited, as well as to determine which design factors proved influential in those differences we ran two separate General Linear Model ANOVAs with Competition Type (Intraspecific, Interspecific), Residency Status (Resident, Intruder), and Species (TM, LG, LM, LP) as fully-fixed and fully-crossed factors. The response variables for the GLM ANOVAs were each individual fish's aggression and boldness measures, respectively, from all of the trials conducted with microhabitat 1. Both response variables were square-root transformed prior to utilization in the ANOVAs in an attempt to normalize the data. Additionally, simultaneous Tukey's Honestly Significant Difference tests were conducted on the models' significant main and interaction effects with a global  $\alpha$ -level set at .05.

##### *Scramble competition*

To determine whether the specific patterns of aggression and boldness observed between species utilized in the scramble trials were significant we used separate two-sample *t*-tests to evaluate square-root transformed raw data. To evaluate our hypothesis that increased aggression in *T. mariae* resulted in improved territorial acquisition as compared to *Lepomis* sunfishes we tested the correlation between individual aggression and dominance.

## Results

### Interspecific territorial competition

With respect to aggression, ‘Residency Status’ and ‘Species’ main effects were significant (Table 1). Residents were more aggressive than intruders (Fig. 2a). Simultaneous Tukey’s HSD tests showed *T. mariae* were more aggressive than *Lepomis* sunfishes, while no differences were noted amongst sunfish species (Fig. 2b). ‘Habitat’ did not have an effect on the levels of aggression in interspecific residency trials.

The interaction effect between ‘Residency Status’ and ‘Species’ was the only significant one (Table 1). This effect was driven by increased aggression by *T. mariae* residents over all other groups (Fig. 3). Levels of aggression amongst *Lepomis* sunfish residents were indistinguishable, but were greater than that of all intruder groups. The aggressiveness of *T. mariae* and each of the *Lepomis* sunfishes were all indistinguishable from one another as intruders.

With respect to boldness, ‘Residency Status’ and ‘Species’ main effects were significant as they were for aggression (Table 2). Residents proved bolder than intruders (Fig. 4a). Simultaneous Tukey’s HSD tests showed *T. mariae* were bolder than *Lepomis* sunfishes, while no differences were noted amongst sunfish species (Fig. 4b). Once again, habitat did not have an effect on the levels of boldness in interspecific residency trials.

The interaction effect of ‘Residency Status’ and ‘Species’ was the only significant one (Table 2). *T. mariae* and each of the *Lepomis* sunfishes were bolder as residents than each of the intruder groups, but were not significantly different from one another

(Fig. 5). *T. mariae* intruders proved bolder than each of the three groups of *Lepomis* sunfish intruders, while no differences existed amongst *Lepomis* sunfish intruders.

With respect to dominance, out of 120 trials, 101 (84.2%) featured the maintenance of dominance by residents over their territory against interspecific intruders. This included 100% of *T. mariae* residents ( $N = 60$ ), and 68.3% of *Lepomis* sunfish residents ( $N = 60$ ; 23 of 36 *L. gulosus*, 6 of 12 *L. macrochirus*, 12 of 12 *L. punctatus*). Of the remaining 19 trials, 18 (15%) resulted in dominance by an interspecific intruder, forcibly evicting residents from established territories (no dominance was exerted by either individual in the remaining trial). All of these evictions were forced by *T. mariae* against either *L. gulosus* or *L. macrochirus*. In all, 30% of *T. mariae* intruders became dominant and expelled *Lepomis* sunfish residents from their territories. Furthermore in these interspecific residency trials, there is a 78.9% correlation between aggression and dominance (Pearson’s correlation using transformed aggressive contact data;  $P < .001$ ,  $N = 240$ ); more aggressive individuals are likely to establish and hold territories, and exclude competitors than less aggressive individuals.

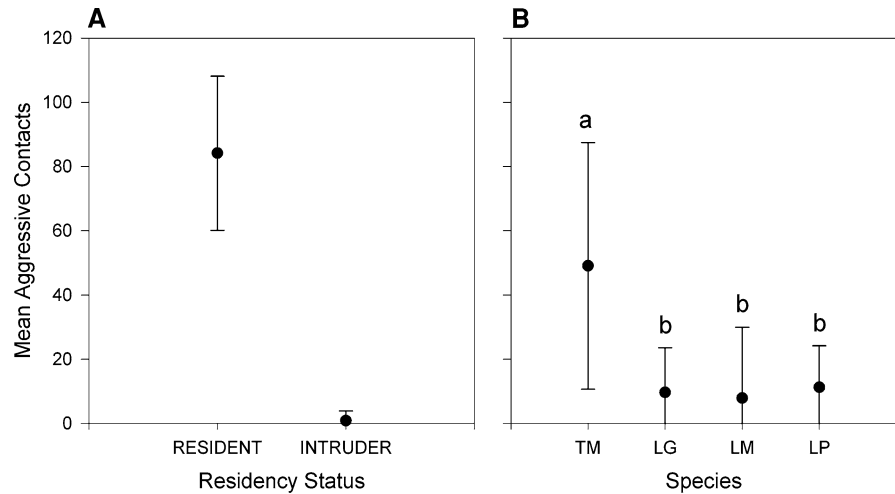
### Intraspecific versus interspecific competition comparison

With respect to aggression, ‘Competition Type’, ‘Residency Status’, and ‘Species’ main effects were all significant (Table 3). More aggressive contacts are logged in intraspecific than interspecific contests. Residents are more aggressive than intruders. Simultaneous Tukey’s HSD tests revealed that *T. mariae*

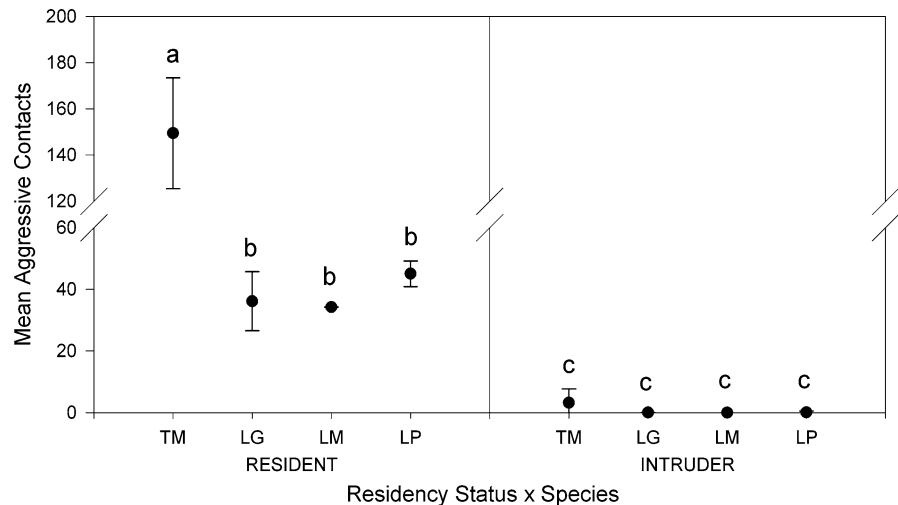
**Table 1** Interspecific territorial competition ANOVA for aggression

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Residency status	1	4,077.75	1,980.13	1,980.13	231.53	<.001
Habitat	2	47.36	26	13	1.52	.221
Species	3	921.2	916.27	305.42	35.71	<.001
Res. status × habitat	2	46.32	46	23	2.69	.07
Res. status × species	3	290.69	289.83	96.61	11.3	<.001
Habitat × species	6	8.7	8.7	1.45	.17	.985
Error	222	1,898.66	1,898.66	8.55		
Total	239	7,290.69				

**Fig. 2** Interspecific residency ANOVA significant main effects plots for aggression. Means were calculated from square-root transformed aggressive contact count data and back-transformed for graphing. **a** Residency status. **b** Species. Simultaneous Tukey's HSD test significant differences indicated above means



**Fig. 3** Interspecific residency ANOVA significant interaction effects plots for aggression. Means were calculated from square-root transformed aggressive contact count data and back-transformed for graphing. Residency status  $\times$  species. Simultaneous Tukey's HSD test significant differences indicated above means



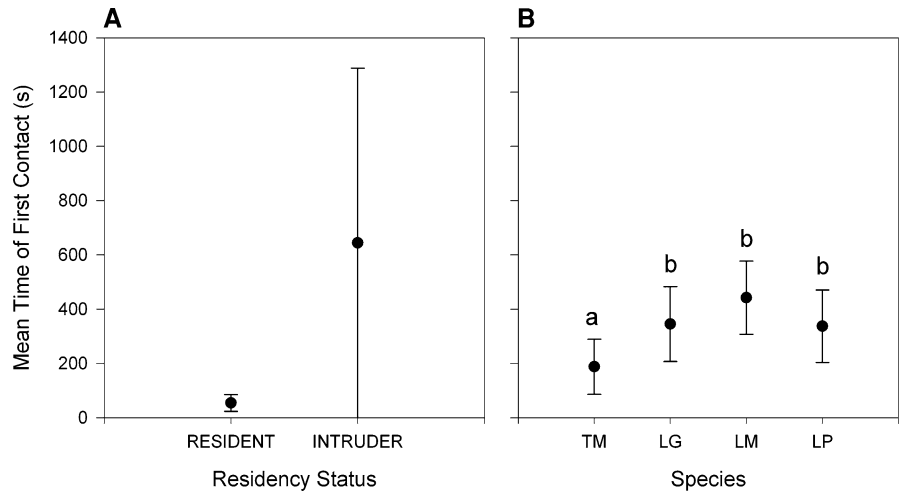
**Table 2** Interspecific territorial competition ANOVA for boldness

Source	DF	Seq SS	Adj SS	Adj MS	<i>F</i>	<i>P</i>
Residency status	1	19,408	14,401.9	14,401.9	403.78	<.001
Habitat	2	12.1	41	20.5	.58	.563
Species	3	1,801.6	1,845.5	615.2	17.25	<.001
Res. status $\times$ habitat	2	70.4	70.4	35.2	.99	.374
Res. status $\times$ species	3	487.1	494.1	164.7	4.62	.004
Habitat $\times$ species	6	166.9	166.9	27.8	.78	.586
Error	222	7,918.2	7,918.2	35.7		
Total	239	29,864.2				

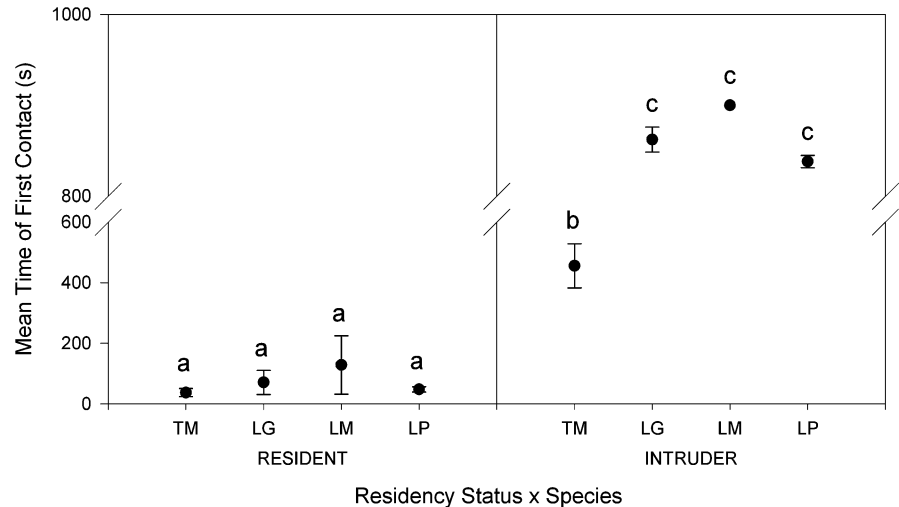
acted more aggressively than each of the three *Lepomis* sunfish species, while no differences in aggression existed amongst the sunfish species themselves.

The interaction effects between 'Competition Type' and 'Residency Status' and 'Residency Status' and 'Species' were also significant (Table 3). The significant interaction between 'Competition Type'

**Fig. 4** Interspecific residency ANOVA significant main effects plots for boldness. Means were calculated from square-root transformed time of first contact data and back-transformed for graphing. **a** Residency status. **b** Species. Simultaneous Tukey’s HSD test significant differences indicated above means



**Fig. 5** Interspecific residency ANOVA significant interaction effects plots for boldness. Means were calculated from square-root transformed time of first contact data and back-transformed for graphing. Residency status × species. Simultaneous Tukey’s HSD test significant differences indicated above means



and ‘Residency Status’ is driven by greater resident aggression in intraspecific than interspecific competitions. Residents engaged in interspecific competition were also more aggressive than intruders. Intruder aggression levels, on the other hand, are comparable regardless of competition type. The significant interaction between ‘Residency Status’ and ‘Species’ was driven by increased aggression in all species as residents over most intruders. *T. mariae* residents in particular were the most aggressive group. Each of the three *Lepomis* sunfish species displayed comparable levels of aggression relative to each other as residents. *Lepomis* residents proved more aggressive than *T. mariae* intruders and *Lepomis* intruders, with the exception of *L. punctatus* residents whose aggression levels did not differ from

*L. macrochirus* intruders. There were no differences in levels of aggression by different species as intruders.

With respect to boldness, ‘Residency Status’ and ‘Species’ main effects were significant (Table 4). Residents were bolder than intruders. Simultaneous Tukey’s HSD tests revealed significant differences between *T. mariae* and two of the three *Lepomis* sunfishes: *L. macrochirus* and *L. punctatus*. No difference was found between *T. mariae* and *L. gulosus* or amongst any set of sunfishes. Boldness did not vary between intraspecific and interspecific contests.

The interaction effect between ‘Competition Type’ and ‘Species’ was the only significant one (Table 4). This effect was driven by increased boldness in *T. mariae* in interspecific encounters compared to

**Table 3** Intraspecific versus interspecific competition comparison ANOVA for aggression

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Competition type	1	178.93	93.51	93.51	7.59	.007
Residency status	1	3,580.32	1,615.7	1,615.7	131.08	<.001
Species	3	528.56	545.88	181.96	14.76	<.001
Comp. type × res. status	1	120.28	110.55	110.55	8.97	.003
Comp. type × species	3	56.09	48.68	16.23	1.32	.271
Res. status × species	3	236.87	236.87	78.96	6.41	<.001
Error	147	1,811.93	1,811.93	12.33		
Total	159	6,512.97				

*L. gulosus* and *L. macrochirus* in interspecific encounters. No other groups differed significantly with respect to boldness.

#### Scramble competition

As individual sunfish species did not vary in aggression or boldness in the interspecific residency trials, they were pooled together in the smaller scramble trials as *Lepomis* sunfish. *T. mariae* were more aggressive than *Lepomis* sunfish in scramble competition for space ( $P < .001$ ,  $N = 38$ ; two-sample *t*-test). *T. mariae* were also bolder than *Lepomis* sunfish in this scenario ( $P < .001$ ,  $N = 38$ ; two-sample *t*-test).

Of 19 trials (one was excluded because of camera malfunction), 15 (78.9%) resulted in *T. mariae* establishing dominance over *Lepomis* sunfishes when both were introduced to a new territory simultaneously. In the four remaining trials (21.1%), neither individual established dominance; *Lepomis* sunfishes failed to establish dominance in all scramble trials. The correlation between aggression and dominance was

extremely similar to that found in the interspecific residency trials, persisting in the scramble scenario at 86.7% (Pearson's correlation using transformed aggressive contact data;  $P < .001$ ,  $N = 38$ ).

#### Discussion

There has been a paucity of studies focused on the impacts on native fishes resultant from competitively-induced spatial alterations caused by non-native fishes (Taylor et al. 1984). Since spatial alterations are a behaviorally-mediated phenomena (Taylor et al. 1984), this dearth of knowledge likely contributes to the continued lack of importance placed on animal behavior in assessing the potential impacts of non-native species. This study is among the first to explore some of the potential ecological effects of behavioral interactions of native North American fishes and introduced tilapiines, a group whose range is increasing throughout the southern US. In doing so, we also provide the first empirical evidence for competitively-induced

**Table 4** Intraspecific versus interspecific competition comparison ANOVA for boldness

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Competition type	1	42.35	104.6	104.6	2.14	.146
Residency status	1	9,493.52	6,573.75	6,573.75	134.49	<.001
Species	3	709.93	732.44	244.15	4.99	.003
Comp. type × res. status	1	73.74	78.63	78.63	1.61	.207
Comp. type × species	3	727.47	728.99	243	4.97	.003
Res. status × species	3	180.47	180.47	60.16	1.23	.301
Error	147	7,185.39	7,185.39	48.88		
Total	159	18,412.88				



spatial displacement of *Lepomis* sunfishes by *T. mariae*. Our results suggest that enhanced interspecific aggression has likely contributed significantly to the invasion success of *T. mariae* in South Florida. Moreover, the ecological effects caused by direct territorial interactions between native and non-native fishes may be vastly underestimated.

The focus of this study was to determine the potential for territorial competition between non-native *T. mariae* and native *Lepomis* sunfishes in South Florida. Our laboratory trials demonstrate that *T. mariae* and *Lepomis* sunfishes compete for territory when space is a limiting factor. As *T. mariae* are significantly more aggressive and bolder than their *Lepomis* sunfish counterparts, they have an advantage in the acquisition and retention of territories. *T. mariae* are entirely able to defend their territories from intruding *Lepomis* sunfishes while usurping up to 30% of established *Lepomis* sunfish territories at any given time. Additionally, *T. mariae* outcompete *Lepomis* sunfishes for new territories with nearly 80% of new territories being dominated by *T. mariae* and the other 20% remaining unclaimed. This competitive advantage is unaffected by the structure of the habitats within which these interactions occur. Thus, *T. mariae* might affect the suitability and availability of *Lepomis* sunfish spawning sites in artificial and natural habitats throughout South Florida, at least at local scales.

Interspecific competition for resources such as food or territory can result in the exclusion of competitively-inferior species by superior species when there is high overlap in utilization (Lawlor and Smith 1976; Pimm and Rosenzweig 1981; Mooney and Cleland 2001). It follows that individual growth rates and population densities of competitively-inferior species are likely to become depressed as a result of competition and niche displacement following the introduction of competitively-superior species (Taylor et al. 1984; Lockwood et al. 2007). If *T. mariae* and *Lepomis* sunfishes preferentially select similar spawning sites in the wild and these sites are limited, then the superior capability of *T. mariae* to establish territories and evict interspecific competitors from these sites may directly affect sunfish fitness.

As *Lepomis* sunfishes serve a role structuring small fish and invertebrate assemblages (Loftus and Kushlan 1987), the Everglades and Big Cypress ecosystems may be particularly susceptible to ecological disruption via the competitively-induced spatial

displacement of these important predators by *T. mariae*. Conditions in both ecosystems may favor their continued increase in population, further increasing the likelihood of significant impacts. First, while most invasive fish species are limited to altered waterways, non-native detritivores (i.e., *T. mariae*) tend to find success in unaltered aquatic systems because these systems rarely lack sufficient quantities of food (Moyle and Light 1996). Second, while *T. mariae* densities have been reduced in the canal system because of the deliberate introduction of Butterfly Peacock (*Cichla ocellaris*) for biological control, *C. ocellaris* is physiologically restricted to canals. Contrary to expectations, *T. mariae* densities in the natural wetlands of Everglades National Park and Big Cypress National Preserve may grow to exceed those in adjacent canals.

Nevertheless, to conclude that *T. mariae* are impacting *Lepomis* sunfish populations the following information is required: (1) Field verification that *Lepomis* sunfishes and *T. mariae* preferentially spawn in similar sites, (2) evaluation of the quantity and quality of potential spawning sites in the region, (3) evidence of habitat shifts in spawning site selection by sunfish in the presence of *T. mariae*, and (4) quantification of the fitness costs on sunfish populations relegated to suboptimal spawning sites. Further investigation into these aspects of *T. mariae* and *Lepomis* sunfish interactions will provide an additional case-study to guide the continued development of the much-needed synthesis of behavioral and invasion ecology.

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