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# Antipredator Responses by Native Mosquitofish to Non-Native Cichlids: An Examination of the Role of Prey Naiveté

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1 Antipredator responses by native mosquitofish to non-native cichlids: an examination of the role  
2 of prey naiveté

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24 **Abstract**

25         The strong impact of non-native predators in aquatic systems is thought to relate to the  
26 evolutionary naiveté of prey. Due to isolation and limited dispersal, this naiveté may be  
27 relatively high in freshwater systems. In this study, we tested this notion by examining the  
28 antipredator response of native mosquitofish, *Gambusia holbrooki*, to two non-native predators  
29 found in the Everglades, the African jewelfish, *Hemichromis letourneuxi*, and the Mayan cichlid,  
30 *Cichlasoma urophthalmus*. We manipulated prey naiveté by using two mosquitofish populations  
31 that varied in their experience with the recent invader, the African jewelfish, but had similar  
32 levels of experience with the longer-established Mayan cichlid. Specifically, we tested these  
33 predictions: (1) predator hunting modes differed between the two predators, (2) predation rates  
34 would be higher by the novel jewelfish predator, (3) particularly on the naive population where  
35 jewelfish have not invaded yet, (4) antipredator responses would be stronger to Mayan cichlids  
36 due to greater experience and weaker and/or ineffective to jewelfish, and (5) especially weakest  
37 by the naive population. We assayed prey and predator behavior and prey mortality in lab  
38 aquaria where both predators and prey were free-ranging. Predator hunting modes and habitat  
39 domains differed, with jewelfish being more active search predators that used higher parts of the  
40 water column and less of the habitat structure relative to Mayan cichlids. In disagreement with  
41 our predictions, we found that predation rates were similar between the two predators,  
42 antipredator responses were stronger to African jewelfish (except for predator inspections), and  
43 there was no difference in response between jewelfish-savvy and jewelfish-naive populations.  
44 These results suggest that despite the novelty of introduced predators, prey may be able to  
45 respond appropriately if non-native predator archetypes are similar enough to those of predators

46 prey experience, if prey rely on general antipredator responses or predation cues, and/or show  
47 neophobic responses.

48 **Key words:** predation, evolutionary naiveté, antipredator behavior, fish, invasion

49 **Introduction**

50 Species invasions that cause high impact to invaded communities often result from novel  
51 intertrophic interactions such as predation (Kats & Ferrer 2003; Gurevitch & Padilla 2004; Salo  
52 et al. 2007). By novel, we mean interactions where the predator has no common evolutionary  
53 history with native prey, resulting in prey that are evolutionarily naive to the introduced  
54 predators (Diamond & Case 1986; Cox & Lima 2006). An extreme form of novelty is illustrated  
55 by the introduction of predators to oceanic islands (and Australia), where predation itself may be  
56 novel or the predator archetype is absent (Ogutu-Ohwayo 1990; Fritts & Rodda 1998; Blackburn  
57 et al. 2004). A less severe and perhaps more common form of novelty stems from variation in  
58 predator archetypes, where native and non-native predators exhibit varying behavioral and  
59 morphological adaptations for prey capture (Cox & Lima 2006). For instance, variation in  
60 predator hunting mode (Schmidt 2007) among native and non-native predators could result in  
61 prey experiencing some degree of predator novelty. Under either scenario, the evolutionary  
62 naiveté of native taxa can result in the failure of prey to recognize predation threats, in  
63 inappropriate antipredator responses or in appropriate but ineffective responses (Diamond &  
64 Case 1986; Banks & Dickman 2007).

65 Prey naiveté is hypothesized to be partly responsible for the strong negative effects of  
66 introduced aquatic predators (Cox & Lima 2006). Dispersal by aquatic top predators is relatively  
67 low and isolation at intercontinental and regional scales can be high in freshwater systems,  
68 resulting in significant variation in predator archetypes and regimes among and within water  
69 bodies. For instance, hydrological gradients can result in small-scale variation in predation  
70 regimes (Wellborn et al. 1996) that should generate prey naiveté to predators that are allopatric  
71 along the gradient (Cox & Lima 2006). In the Florida Everglades, the recurrent pattern of

72 seasonal dry-down limits the abundance of large-bodied predators both temporally and spatially  
73 (Chick et al. 2004; Trexler et al. 2005), which may result in gradients in naiveté that accompany  
74 hydrological gradients across the landscape (i.e., long vs. short hydroperiod marshes), although  
75 this remains untested.

76 Another and perhaps more important source of gradients in prey naiveté is the patchiness  
77 in the distribution of non-native predators. The African jewelfish, *Hemichromis letourneuxi*, one  
78 of the most recent invaders of the Everglades, is presently limited to the southern and western  
79 regions of the ecosystem (Shafland et al. 2008). Jewelfish were first detected in Everglades  
80 National Park (ENP) in 2000 (J. Kline pers. comm.) and are presently undergoing a rapid range  
81 expansion into longer hydroperiod marshes and mangrove regions (Shafland et al. 2008, Rehage  
82 et al. unpubl. data), but have not yet colonized marshes in the Water Conservation Areas in the  
83 northern Everglades. They are piscivores, with fish accounting for 70-80% of their diet (Loftus et  
84 al. 2006). Their small size allows them to invade shallower habitats, where larger invaders have  
85 previously been excluded, and thus they are an especially concerning invader. Among the more  
86 established invaders of the Everglades is the Mayan cichlid, *Cichlasoma urophthalmus*, first  
87 detected in 1983 in ENP and presently widespread throughout the system (Loftus & Kushlan  
88 1987; Fuller et al. 1999; Shafland et al. 2008). Mayan cichlids can be a dominant component of  
89 the fish community of certain habitats. In particular, they can account for up to 40% of fish  
90 abundance in the mangrove zone (Trexler et al. 2001). They are also predators, with fish being a  
91 dominant prey item in their diets (Bergmann & Motta 2005). These two cichlids invaders are  
92 currently the two most abundant fish invaders in ENP out of about 14 established species  
93 (Shafland et al. 2008; J. Kline pers. comm.), and thus have the potential to have a high impact on  
94 invaded aquatic communities. How native Everglades prey, particularly small-fish taxa, cope and

95 respond to these predation threats that vary in the degree of novelty is currently unexplored.  
96 Furthermore, although prey naiveté is invoked as a major mechanism for the high impact of  
97 introduced predators, few studies have examined it directly (Cox & Lima 2006).

98         In this study, we used laboratory assays to examine the effect of predator novelty and  
99 prey naiveté on predator-prey interactions between native Everglades prey and non-native cichlid  
100 predators. Specifically, we quantified the antipredator behavior of native Eastern mosquitofish  
101 (*Gambusia holbrooki*), and the hunting mode, habitat domain and lethality of the Mayan cichlid  
102 and African jewelfish. Mosquitofish are the most ubiquitous fish species in the Everglades  
103 (Trexler et al. 2005), and should be readily encountered and consumed by both predators. In fact,  
104 stomach analyses of African jewelfish from our study sites in ENP show that mosquitofish are  
105 the most abundant prey item (Loftus et al. 2006). Predation by non-native predators on  
106 ubiquitous prey such as mosquitofish may lead to invaders having wide-ranging impacts.  
107 Moreover, we expect ubiquitous prey to have important functional roles throughout the system,  
108 and if non-native predators are able to significantly decrease their abundance, this could also  
109 contribute to high impacts in the invaded system. We manipulated the degree of novelty in  
110 predator-prey interactions by using these two predator species that varied in the time since  
111 invasion, and mosquitofish populations that varied in experience with them. We hypothesized  
112 that variation in the hunting modes and habitat domain of the predators would make jewelfish a  
113 relatively novel predation threat. Due to the greater naiveté of Everglades prey with African  
114 jewelfish, we expected predation rates to be higher by this novel predator. We hypothesized that  
115 due to greater experience, the antipredator responses of prey would be stronger to the Mayan  
116 cichlid. We compared mosquitofish populations with the expectation that prey from jewelfish-  
117 invaded areas would exhibit greater and/or more effective antipredator responses to jewelfish

118 than naive prey from areas where jewelfish are absent, and thus jewelfish predation would be  
119 higher on the naive population.

120

## 121 **Methods**

122 To examine the predatory behavior and effect of the cichlids species and the antipredator  
123 response of mosquitofish, we conducted behavioral assays in laboratory aquaria. In a 4 x 2  
124 factorial design, we observed the effects of four predation treatments on two mosquitofish prey  
125 populations. Predation treatments consisted of predator pairs in a replacement series design  
126 where predator density remained constant (Sih et al. 1998). Treatments included: (JJ) 2 African  
127 jewelfish, (MM) 2 Mayan cichlids, (MJ) 1 African jewelfish + 1 Mayan cichlid, and (NP) no  
128 predators. Mosquitofish were collected from two populations that varied in their naiveté to  
129 African jewelfish, but had similar levels of experience with Mayan cichlids. The ENP  
130 mosquitofish population was considered ‘experienced’ since African jewelfish have been present  
131 and abundant for close to a decade. A second prey population from northern Water Conservation  
132 Area 3A (WCA3A) was considered naive to African jewelfish since despite repeated sampling  
133 by ourselves and colleagues over the past few years, they have never been collected there or that  
134 far north in the inner Everglades ecosystem. Both populations should have similar levels of  
135 experience with Mayan cichlids, which have been present and abundant throughout since the  
136 1980’s.

137 Trials were conducted in two blocks in July 27-30, 2007 and March 3-8, 2008,  
138 corresponding to the wet and dry seasons in the Everglades respectively (hereafter referred to as  
139 the season effect). A minor objective of our study was to examine whether predator motivation  
140 and antipredator behavior would vary seasonally in response to dry-down and the expected



141 physiological stress associated with it (i.e., reduced prey abundance and poor condition).  
142 Cichlids were collected from the Rocky Glades region of ENP using unbaited minnow traps  
143 deployed overnight in June-July 2007 and January-February 2008. Mosquitofish were collected  
144 using dip nets at a WCA3A site (N 26.147, W 80.57134) and at the same ENP Rocky Glades  
145 locations where predators were collected. Predator species were size-matched in trials, but  
146 because of species-specific size differences, African jewelfish were adults ( $51.7 \pm 0.9$  mm  
147 standard length), while Mayan cichlids were juveniles of approximately  $65.6 \pm 1.8$  mm standard  
148 length. Bergmann & Motta (2005) showed that fish remain the primary prey item for Mayan  
149 cichlids throughout development. All prey used in the study were juveniles ( $13.1 \pm 0.2$  mm  
150 standard length). Prior to the experiment, we held predators and prey in 795-l outdoor tanks and  
151 fed them a combination of live prey, including mosquitofish from both populations. We fed prey  
152 flakes *ad libitum*.

153         In both seasons, trials were conducted over 4 consecutive days. Each day, we tested a  
154 single replicate of the 8 treatment by population combination (4 treatments x 2 prey populations  
155 x 4 days x 2 seasons = 64 experimental units). To minimize inter-individual variation in predator  
156 motivation, randomly-assembled predator pairs were used repeatedly with the two prey  
157 populations. Pairs were randomly assigned to days 1 or 2 of the block and then used again in day  
158 3 and 4 respectively with a different prey population. For instance, a predator pair that  
159 experienced the ENP prey population on day 1, was assigned to the WCA3A mosquitofish  
160 population on day 3, and similar for day 2 and 4. Trials were not conducted on consecutive days  
161 in order to obtain overnight prey mortality rates and then standardize hunger levels prior to the  
162 next trial. This protocol was repeated with a new set of predators in the dry season, for a total  
163 number of 24 jewelfish and 24 Mayan predators used in the study.

164 For each trial, behavioral data were collected on a group of 6 mosquitofish (6 prey x 4  
165 treatments x 2 populations x 8 replicates = 384 prey). Mosquitofish groups from both  
166 populations were isolated in 5.7-l containers the evening prior and then randomly assigned to  
167 treatments on the day of trials. Similarly, predators were isolated in 5.7-l containers the evening  
168 before trials and between trials. To standardize hunger levels, all feeding was suspended 24 h  
169 before trials, as well as between trials for the predators (e.g., no feeding on day 2 for a predator  
170 used on days 1 and 3).

171 Trials were conducted in 8 56.8-l aquaria (50 x 24.5 x 40 cm height) covered on all 4  
172 sides with white vinyl. Artificial vegetation was used to provide structural complexity for both  
173 predators and prey (16 x 16 cm, covering approximately 1/3 of tank area). This artificial  
174 vegetation consisted of black plastic strips (4 x 22 cm) attached to a weighted plastic grid that  
175 rested on the bottom and to one side of each tank. To minimize observer effects, observations  
176 were conducted through mirrors placed at 45° angles above tanks. At the beginning of each trial,  
177 prey were released and allowed to acclimate for 15 min before predators were added. The first  
178 observation was taken 5 min after predator release.

179 Prey and predator behavior was assessed through spot-check observations conducted by  
180 two observers, one taking data on the predators and the other on the prey (Martin & Bateson  
181 2007). Observers spent 20-60 s per tank accounting for all individuals and noting their activity,  
182 microhabitat use, and the shoaling behavior of prey. Ten spot-check observations were  
183 conducted per tank, one every 10-12 min for a total trial duration of approximately 2 h. All  
184 observations were conducted between 10 AM-1 PM. Activity was scored as active if there was  
185 movement that resulted in a change in position (e.g., movement of fins was scored as inactivity).  
186 For microhabitat use, we noted vertical distribution within the tank (top, middle or bottom one

187 third of the water column), and whether predators and prey were in or out of the habitat structure.  
188 For these three variables, we calculated the proportion of predators and prey engaged in each  
189 behavior over the 10 observations and then averaged them. Shoaling behavior by mosquitofish  
190 was scored as a 1 if prey were aggregated in a social group of at least 4 individuals (within  
191 approximately 4 body lengths of each other); otherwise it was scored as a 0, and then scores were  
192 averaged over the 10 observations. At the end of the spot-check observations, tanks were  
193 observed continually for 5 min to obtain count data on the attacks on prey and predator  
194 inspections. Rapid approaches by predators to the prey with or without contact were considered  
195 attacks. Predator inspections consisted of cautious approaches by prey, followed by a rotation or  
196 retreat of the prey while still visually fixated on the predator. Actual predation events during this  
197 observation period occurred in only 3 of the 64 trials for a total of 9 prey consumed.

198 At the end of all behavioral observations, we assessed mortality rates of the prey in the  
199 same observation tanks. In order to avoid prey depletion, an additional 6 prey (of the same size  
200 and population) were added to each tank. In the few cases where prey were consumed during the  
201 observation period, we replaced them in order to begin all replicates with 12 mosquitofish. We  
202 left predators and prey in covered tanks overnight, and between 7-8 AM on the following day,  
203 we uncovered tanks and counted the number of surviving prey. Photoperiod over the study was  
204 set to 14L:10D, and water temperature averaged  $25.7 \pm 0.18$  ° C.

## 205 Statistical analyses

206 Population differences among predator treatments were examined with linear models. In  
207 addition to population and treatment main effects, we tested the effects of the population by  
208 treatment interaction, of season (the blocking factor), and of predator pair nested within season to  
209 account for the repeated used of predators. These same effects were tested in two MANOVAs

210 ran prior to the ANOVAs. A MANOVA was run for the five focal prey variables for which data  
211 were collected in all treatments: the proportion of prey active, at the top of the water column and  
212 using the habitat structure, the occurrence of prey shoals, and prey mortality. A second  
213 MANOVA was run for the remaining five focal variables that involved predators and for which  
214 data were collected only in the three predation treatments: the proportion of predators active, at  
215 the top of the water column, and using the habitat structure, and the number of predator attacks  
216 and inspections. Preliminary analyses also examined the effect of predator sequence (day 1 vs. 3,  
217 and day 2 vs. 4), and of the sequence by season interaction on all response variables and found  
218 little effect; therefore, these factors were removed from final analyses reported here. Predator  
219 sequence only affected two of the predator variables and none of the prey variables, and the  
220 effect was seen only in the dry season, in which predators spent more time at the top of the water  
221 column and less time in the habitat structure on day 3 and 4 relative to day 1 and 2.

222 To meet parametric test assumptions, we examined the behavior of residuals and  
223 transformed variables where evidence of non-normality and variance heterogeneity was found,  
224 which included all variables except prey mortality (Kery & Hatfield 2003). Angular  
225 transformations were applied to proportions and log transformations ( $\ln$  of observed value + 1)  
226 to counts. Tukey pairwise comparisons were used to compare treatment and treatment by  
227 population means. All statistical tests were conducted using the GLM procedure in SAS® 9.1.3.

228

## 229 **Results**

### 230 *Prey behavior*

231 The antipredator behavior of mosquitofish varied to a greater extent as a function of  
232 predator treatments than populations. Little variation in antipredator behavior was detected

233 between jewelfish-naive (WCA3A) and jewelfish-experienced (ENP) populations. The exception  
234 was prey activity, which was high overall, and relatively higher in the ENP population (98%  
235 active relative to 92% in WCA3A population, Fig. 1A), but was unaffected by predator treatment  
236 (Table 1).

237         The presence of predators resulted in shifts in microhabitat use by prey. Mosquitofish  
238 were found higher in the water column if the predators were African jewelfish or mixed (Tukey  
239 pairwise comparisons: JJ vs. MM and NP,  $p < 0.0001$ ; MJ vs. MM and NP,  $p < 0.0004$ ). Over  
240 80% of prey were observed in the top 1/3 of the water column in JJ and MJ treatments compare  
241 to only 48% in MM and 30% in NP treatments (Fig. 1B). Prey tended to use the habitat structure  
242 more if predators were absent than if predators were the Mayan cichlid pair since Mayan cichlid  
243 use of the structure was relatively high (Table 1, Fig. 1C).

244         Mosquitofish shoaled more in the presence of predators (NP vs. JJ, MM and MJ,  $p <$   
245  $0.0248$ , Table 1). Shoals were also more common with the jewelfish pair (JJ vs. MM,  $p =$   
246  $0.0058$ ). The occurrence of shoals averaged 63% with the jewelfish pair, 41% with the Mayan  
247 pair, and only 18% in the no predator treatment (Fig. 2). Shoaling rates did not vary between the  
248 single and mixed predator treatments. Shoaling was the only variable that varied between blocks  
249 (higher in the dry season, Table 1). Despite the fact that mosquitofish appeared to respond more  
250 strongly to jewelfish predators with their shoaling behavior and greater use of the top of the  
251 water column, predator inspections by both prey populations were higher on the less novel  
252 Mayan predators (MM vs. JJ and MJ,  $p < 0.0335$ , Fig. 3).

253

254 *Predator behavior*

255 African jewelfish and Mayan cichlids varied in their activity and microhabitat use,  
256 suggesting variation in hunting modes and habitat domains. Their behavior was also unaffected  
257 by the degree of novelty of the prey; predator behavior was similar toward the ENP and WCA3A  
258 mosquitofish populations (Table 1). Predator activity was highest for the jewelfish pair,  
259 intermediate for the mixed predator treatment and lowest for the Mayan pair (Table 1, all  
260 pairwise comparisons,  $p < 0.0064$ ; Fig. 1A). Jewelfish pairs also spent more time in the upper  
261 water column and less time in habitat structure relative to the Mayan pairs (JJ vs. MM,  $p <$   
262  $0.0005$  for both comparisons; Figs. 1B and C). The vertical distribution of predators was affected  
263 by predator identity (Table 1). Certain predator pairs spend more time high in the water column  
264 than others.

265

#### 266 *Prey mortality*

267 Despite variation in predator behavior and the prey response, predator voracity and  
268 lethality were similar among predator combinations. The number of attacks on prey at the end of  
269 trials was low, on average one attack per 5-minute observation period, and did not differ among  
270 treatments (Table 1). Similarly, overnight predation rates were comparable across predator  
271 combinations and between the two prey populations (Table 1). On average, predators consumed  
272 8 mosquitofish relative to zero mortality in the control tanks (Fig. 4).

273

#### 274 **Discussion**

275 The prey naiveté hypothesis suggests that the high impact of aquatic predators relates to  
276 prey's limited ability to detect and respond to novel predation threats posed by non-native  
277 piscivores (Cox & Lima 2006). Our results did not find support for this notion. First, predator

278 avoidance responses by mosquitofish appeared stronger to the more novel predation threat, the  
279 African jewelfish, relative to those exhibited toward Mayan cichlids. Mosquitofish responded by  
280 altering their microhabitat use, increasing shoaling, and examining predators. Despite prey  
281 engaging in these behaviors in the presence of jewelfish, mortality rates were similar between the  
282 two predators. No variation in attack rates and overnight predation rates was detected, although  
283 predator microhabitat use and activity varied. Little variation was found between the seasons  
284 (blocks) suggesting that the characteristic seasonal hydrological variation of the Everglades  
285 ecosystem may have little effect on the predator and prey behaviors examined here, although our  
286 power to detect this effect was likely low.

287         Second, the amount of naiveté of mosquitofish populations did not appear to affect their  
288 antipredator response. The response to jewelfish was as strong by the naive WCA3A  
289 mosquitofish population, which had no experience with jewelfish, than by the ENP population,  
290 where jewelfish occur and pose a significant predation threat to mosquitofish (Loftus et al.  
291 2006). Confirmation of this result with a larger number of experienced and naive prey  
292 populations is needed. Examination of this question with other prey species is also needed. Our  
293 own examination of the response of other Everglades prey to novel African jewelfish shows that  
294 antipredator responses are species specific (Dunlop & Rehage, unpubl. data) and may result in  
295 variation in prey vulnerability. Nannini and Belk (2006) found similar variation for the response  
296 of two minnow species to introduced trout.

297         Our experimental design using free-ranging predators and prey allowed us to examine the  
298 response of predators and prey spatially. Prey typically try to avoid areas with high predation  
299 risk, while predators concentrate efforts in areas with more prey. Most studies cage or otherwise  
300 restrict predator movement (Lima 2002), limiting one's ability to examine this behavioral

301 response race (Sih 2005). Mosquitofish did not reduce activity in the presence of predators, but  
302 altered the use of tank microhabitats. In the presence of African jewelfish, prey moved higher in  
303 the water column. Changes in the vertical distribution of mosquitofish in response to predation  
304 risk have been noted in previous studies (Garcia et al. 1992; Smith & Belk 2001). Since both  
305 predators were found relatively low in the water column, this change in microhabitat use likely  
306 reduced their spatial coincidence with predators. With Mayan cichlids, prey minimized  
307 encounters by reducing use of habitat structure in their presence, because Mayan pairs used  
308 cover to the greatest extent. Mosquitofish also increased shoaling behavior in response to  
309 jewelfish but not Mayan cichlids. Shoaling is known to function largely as a defense behavior  
310 since it typically enhances vigilance and predator confusion and abates attacks, allowing for  
311 coordinated evasion and risk dilution (reviewed by Pitcher & Parrish 1993).

312         Prey often engage in the visual inspection of potential predators as a means of assessing  
313 predator identity and motivation (Lima & Dill 1990; Dugatkin & Godin 1992; Brown 2003). In  
314 this study, prey inspections were directed towards Mayan cichlids more than African jewelfish.  
315 This result agrees with previous work showing that experienced prey inspect more than relatively  
316 naive prey (Magurran & Seghers 1990; Kelley & Magurran 2003; but see Brown & Warburton  
317 1999). It is also possible that prey engaged in higher inspections with Mayans cichlids because  
318 Mayans were perceived to be the lower-risk predator. Since inspections involve approaches to  
319 the predator, they can be riskier than other antipredator behaviors (Dugatkin 1992), and prey may  
320 afford to engage in inspection only with relatively low-risk predators (Smith & Belk 2001).  
321 Mayan cichlids were also less active than jewelfish, and previous work shows that all else being  
322 equal, prey are more likely to inspect stationary rather than moving threats (Pitcher et al. 1986;  
323 Dugatkin & Godin 1992). Further, in the presence of the highly-active jewelfish, it may be



324 unnecessary for mosquitofish to engage in inspection to assess risk, as microhabitats with active  
325 predators can become ‘cue-saturated’ (Preisser et al. 2007).

326 Prey seemed to respond to the two cichlid predators with both different antipredator  
327 tactics and different magnitudes of response. The increase in shoaling and use of the upper water  
328 column shown only with African jewelfish suggest to us that both mosquitofish populations  
329 perceived jewelfish to be the riskier predators, despite their variable experience with them. Prey  
330 altered microhabitat use (either to the top of the water column or out of the structure) when faced  
331 with both predators, but the magnitude of the response (e.g., behavior without predators –  
332 behavior with predators) was much greater in the presence of jewelfish, suggesting higher risk.  
333 The same is seen in the shoaling behavior, shoal sizes are greater in the presence of jewelfish  
334 than in the presence of Mayans. We expect prey to modulate their response to match the  
335 predation threat (i.e., threat-sensitive predator avoidance hypothesis; Helfman 1989; Chivers et  
336 al. 2001; Mirza et al. 2006; Botham et al. 2008) or perception of such risk (Sih 1992; Brown  
337 2003; Lima & Steury 2005).

338 We suspect that the perception of higher risk by jewelfish may relate to the disparity in  
339 predator behavior and predation cue intensity. Brown & Chivers (2005) suggest that predator  
340 movement is a primary visual cue used by prey to distinguish between relevant and irrelevant  
341 threats. Jewelfish were significantly more active than Mayan cichlids and spent more time out in  
342 the open water suggesting an ‘active’ hunting mode (Schmitz 2007, Preisser et al. 2007), which  
343 could have been perceived, even by the inexperienced WCA3A prey, as a more imminent threat  
344 (i.e., a more motivated predator). In contrast, Mayans were less active and remained low in the  
345 water column and in the habitat structure suggesting a ‘sit and wait’ or ‘sit and pursue’ predator  
346 mode (Schmitz 2007), at least in the daytime hours when data were collected. In agreement,

347 experiments that have manipulated predator movement show that prey exhibit stronger  
348 antipredator responses to moving rather than stationary predation threats (Brown & Warburton  
349 1997; Brown & Warburton 1999; Wisenden & Harter 2001).

350         The fact that naive and experienced prey populations had similarly strong antipredator  
351 responses toward African jewelfish is one of the most significant results. Their responses seem to  
352 indicate that both prey populations deemed jewelfish to be the riskier predator; but how did they  
353 arrive to this same perception if WCA3A prey have no experience with jewelfish? We suggest at  
354 least four possible explanations that merit consideration. First, although jewelfish are a new  
355 predator in the Everglades, their predator archetype may not be novel and instead it resembles  
356 common predators mosquitofish encounter enough (i.e., native centrarchids) to allow for prey  
357 recognition and response. However, our data show that their hunting mode is at least different  
358 from one other common non-native predator. Jewelfish are also considerably more active, social  
359 and aggressive than at least one of the abundant Everglades centrarchids examined so far  
360 (*Lepomis gulosus*) (Dunlop & Rehage, unpubl. data; Schofield et al. 2007). Whether the  
361 variation in predator hunting mode and habitat domain seen here generates sufficient predator  
362 novelty to cause prey to fail to respond or respond inappropriately or ineffectively deserves  
363 further study.

364         Second, it is plausible that the WCA3A mosquitofish are exhibiting a general  
365 antipredator response (e.g., multi-predator hypothesis; Blumstein 2006), whereby exposure to  
366 high-risk environments allows prey to develop heightened antipredator responses regardless of  
367 whether or not prey have had experience with particular predators. WCA3A mosquitofish were  
368 collected from a marsh adjacent to the I75 canal. Canals bisecting Everglades marshes provide  
369 key habitat for large-bodied fishes (Rehage & Trexler 2006) and may act to locally increase

370 predation risk for prey in nearby marsh habitats, perhaps allowing prey to develop strong general  
371 antipredator behaviors.

372         Third, naive prey may be able to detect jewelfish as a threat despite their novelty, if they  
373 rely on general predation cues for predator detection and recognition. General cues include  
374 chemical cues associated with predator diet, disturbance cues associated with stressed/startled  
375 prey, and damage-released alarm cues associated with a predator attack (reviewed by Chivers &  
376 Smith 1998; Brown 2003; Wisenden & Chivers 2006). These alarm signals can effectively  
377 'label' potential predators as such. In contrast, native species that rely on specific cues (e.g., the  
378 scent or vocalization of a particular predator) may be unable to recognize and respond to novel  
379 predators (Jones et al. 2004; Smith et al. 2008). Although mosquitofish are known to respond to  
380 the release of conspecific skin extract (Garcia et al. 1992), only a very small number of predation  
381 events occurred, making it unlikely that alarm cues were important. Instead, predators were fed  
382 mosquitofish prior to trials (along with other native prey) and at least closely-related western  
383 mosquitofish (*Gambusia affinis*) can detect predator dietary cues (Smith & Belk 2001).

384         Finally, we suggest that general visual cues could also be used in predator detection  
385 instead or in addition to chemical cues. Prey may be responding to the presence of any novel,  
386 large (above a certain threshold) and moving object (Dill 1974; Brown & Warburton 1997;  
387 Wisenden & Harter 2001). In a sense, this constitutes a neophobic response. Neophobia refers to  
388 the fear of novelty, and is typically characterized by aversion, hesitation or caution (Greenberg  
389 2003). Neophobia may be adaptive when predation risk is very high and/or predator diversity is  
390 low (Brown & Chivers 2005). Under these circumstances, a large moving individual encountered  
391 by prey is likely to be a potential predator, and prey should exhibit antipredator behavior in  
392 response regardless of predator identity. Both of these conditions could apply to our WCA3A

393 prey. As mentioned earlier, marshes nearby canals may experience high predation regimes, and  
394 at same time, the diversity of piscivores in Everglades habitats is relatively low, usually  
395 dominated by seven to eight taxa (Chick et al. 2004; Rehage & Trexler 2006).

396 In conclusion, we note that this study examines the first level of prey naiveté, which  
397 relates to predator detection and recognition (Banks & Dickman 2007) and shows that prey may  
398 be able to overcome it. Cox & Lima (2006) suggest that this may be the most damaging form of  
399 prey naiveté, but we suggest otherwise. A large body of literature shows that prey, particularly  
400 aquatic prey, that often lack innate responses to sympatric predators, can learn to recognize novel  
401 predators very quickly and effectively (i.e. after a single exposure) (Brown & Warburton 1999;  
402 Brown 2003; Brown & Chivers 2005; Mirza et al. 2006), and may be able to generalize this  
403 recognition to related predators (i.e., in the same family; Ferrari et al. 2007). Although not yet  
404 explored greatly, we expect that experience and learning are likely to be key mechanisms  
405 allowing for novel predator detection in invasion scenarios. Instead, the ability of prey to show  
406 appropriate and effective antipredator responses once predators are detected may be more  
407 important in determining large invader impacts. Here, prey are limited by their arsenal of  
408 behavioral responses and other forms of phenotypic plasticity, and this may be a larger obstacle  
409 to overcome than recognition (e.g., Banks et al. 2008). Additional studies are needed to elucidate  
410 the ability of native prey to respond to non-native predators, and the role played by different  
411 levels of prey naiveté in invasive predator impact.

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413

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420

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## Figure legends

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563

564 **Fig. 1:** Effects of predator treatment (JJ = 2 African jewelfish, MM = 2 Mayan cichlids, MJ =  
565 African jewelfish + Mayan cichlid, and NP = no predator) and prey population (WCA3A = naive  
566 and ENP = experienced with African jewelfish-both are experienced with Mayan cichlids) on the  
567 (a) activity level, (b) water column distribution, and (c) use of habitat structure of both predators  
568 and prey. All variables represent the proportion of fish in each behavior (means  $\pm$  SE).

569

570 **Fig. 2:** Shoaling behavior of mosquitofish across predator treatments (JJ= 2 African jewelfish,  
571 MM = 2 Mayan cichlids, MJ = African jewelfish + Mayan cichlid, and NP = no predator) and  
572 prey populations (WCA3A = naive and ENP = experienced to jewelfish-both are experienced  
573 with Mayan cichlids). Groups of 4, 5 or 6 prey were considered a shoal and scored as 1's;  
574 smaller groups were scored as 0's. Shown are means  $\pm$  SE.

575

576 **Fig. 3:** Counts of predator inspections by mosquitofish across predation treatments (JJ = 2  
577 African jewelfish, MM = 2 Mayan cichlids, MJ = African jewelfish + Mayan cichlid, and NP =  
578 no predator) and mosquitofish populations (WCA3A = naive and ENP = experienced with  
579 African jewelfish-both are experienced with Mayan cichlids) over a 5-min. continuous  
580 observation period at the end of trials. Shown are means  $\pm$  SE.

581

582 **Fig. 4:** Overnight mosquitofish mortality rates across treatments (JJ = 2 African jewelfish, MM =  
583 2 Mayan cichlids, MJ = African jewelfish + Mayan cichlid, and NP = no predator) and prey  
584 populations (WCA3A = naive and ENP = experienced with African jewelfish-both are  
585 experienced with Mayan cichlids). Shown are means  $\pm$  SE.

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600 **Table 1:** Result of ANOVAs and MANOVA's (p-values and R<sup>2</sup>) testing predation treatment, population, interaction, **season (or**  
 601 **block)**, and predator pair effects. MANOVA1 contains the 5 variables measured in all treatments, and MANOVA2 contains the 5  
 602 variables measured in the 3 predator treatments only.

		P values for effects				
Variables	R <sup>2</sup>	Treatment	Population	Treatment x Population	Season	Predator pair ( <b>Season</b> )
MANOVA1 Wilks' Lambda		<b>0.0001</b>	0.0945	0.9248	<b>0.0001</b>	0.4322
MANOVA2 Wilks' Lambda		<b>0.0001</b>	0.9567	0.5999	0.6798	<b>0.0522</b>
<i>Prey</i>						
Activity	0.21	0.4318	<b>0.0380</b>	0.4814	0.0932	0.5437
Vertical distribution	0.63	<b>0.0001</b>	0.1262	0.8297	0.5850	0.0992
Use of habitat structure	0.18	0.0571	0.8561	0.7119	0.2182	0.7063
Shoaling behavior	0.64	<b>0.0001</b>	0.4871	0.3419	<b>0.0001</b>	0.5835
Predator inspections	0.32	<b>0.0112</b>	0.7997	0.3269	0.1741	0.1380
Mortality	0.64	<b>0.0001</b>	0.5741	0.9609	0.9655	0.4663

615							
616	<i>Predators</i>						
617	Activity	0.56	<b>0.0001</b>	0.8481	0.2298	0.8780	0.2126
618	Vertical distribution	0.48	<b>0.0001</b>	0.3185	0.7373	0.4942	<b>0.0192</b>
619	Use of habitat structure	0.38	<b>0.0008</b>	0.6445	0.2574	0.7646	0.1892
620	Attacks	0.14	0.2009	0.7829	0.6451	0.3486	0.5315

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