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Recognition of non-native peacock bass, *Cichla kelberi* by native prey: testing the naiveté hypothesis

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Abstract Prey naiveté is proposed as one of the main reasons behind species extinctions attributed to invasive predators. This study examined whether the naiveté hypothesis could explain extinctions after the introduction of peacock bass (*Cichla kelberi*) in Paraná River, Brazil. Our results show that prey responded to both visual and chemical cues of peacock bass. Displayed avoidance behaviors were equal to or greater than those observed with a native predator, *Hoplias malabaricus*. We conclude that lack of recognition was not responsible for the observed vulnerability of native species to this introduced predator. Finally, we discuss implications of these findings for the native biodiversity and convene other potential explanations for the observed effects of peacock bass on native prey.

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Introduction

Co-existence of most predators and prey is possible because prey are capable of reducing their susceptibility to a lethal attack. Most prey use a variety of ways to distinguish subtle changes in predation risk and modify their behavior and habitat use to decrease the probability of detection and capture (Lima and Dill 1990; Brown and Chivers 2005). On the contrary, if prey are unable to recognize and respond to predators, they will experience increased predation mortality (e.g., Mathis and Smith 1993a), a situation that has been referred to as prey naiveté. Prey naiveté may arise from lack of previous ontogenetic exposure to a sympatric predator or, in case of true evolutionary naiveté, result from lack of co-evolutionary history with a certain predator archetype. Due to long periods of isolation and great endemicity of freshwater habitats, this second type of prey naiveté has been implicated in the widespread sensitivity of freshwater organisms to introduced predators (Cox and Lima 2006). These authors define naiveté more generally as lack of effective antipredator defenses, but argue that lack of predator recognition may be

the most serious form of prey naiveté. Species extinctions after introduction of predatory fish (e.g., Nile perch, Witte et al. 1992; peacock bass, Zaret and Paine 1973) indirectly support this hypothesis, and several studies report lack of introduced predator recognition by native prey (Shave et al. 1994; Kiesecker and Blaustein 1997; Smith et al. 2008 but see Nannini and Belk 2006; Stuart-Smith et al. 2008). In order to test the naiveté hypothesis, prey responses to a novel predator type need to be compared to responses to a native predator. Yet, despite its potential importance for understanding invasive predator effects, most studies did not specifically address the naiveté hypothesis, did not explain a priori why the invasive predator in question is expected to represent a novel archetype (sensu Cox and Lima 2006) or fell short of comparing invasive to native predators. Other studies were conducted in depauperate systems (e.g., Shave et al. 1994; Nannini and Belk 2006), where predator impact may result from complex interactions between community undersaturation (sensu Stachowicz and Tilman 2005) and prey naiveté.

We set out to test the prey naiveté hypothesis in a very diverse system with high native predator richness, the Paraná River, which was nevertheless vulnerable to an introduced predator, peacock bass (*Cichla kelberi* Kullander and Ferreira). Peacock bass (*Cichla* spp.) are large piscivorous fish native to the Amazon River and its tributaries in northern South America. As a top predator with high environmental plasticity and parental care, peacock bass was a perfect candidate for a high-impact invasion but was nevertheless introduced in many regions of the world, including Hawaii, southern Brazil and Florida. In Gatun Lake, Panama, *C. ocellaris* completely devastated the native fish assemblage by eliminating 7 out of 11 previously common fish species and significantly reducing three others (Zaret and Paine 1973). More recently, *C. kelberi* introduction in the Rosana Reservoir, upper Paraná River, Brazil resulted in a 95% decline in native fish density and 80% decline in richness in only 2 years (Pelicice and Agostinho 2009).

Amazon-Orinoco system and the Paraná system have been separated for approximately 10 million years (Montoya-Burgos 2003), and the Paraná River historically had high levels of turbidity (Abujanra 2007), which means that peacock bass may indeed be

a novel, visual predator in this system. Peacock bass was first observed in the Paraná River in 1985 and remained at a low density until recently. At present, *Cichla* are found in most reservoirs of the basin (Agostinho et al. 2008). Although their density in the river channel is still relatively low, it seems to be increasing, possibly benefiting from an increase in water transparency and from hydrological alterations after the construction of several large dams (Abujanra 2007). In order to mitigate effects of peacock bass, protect the native species and assess the potential for detrimental impacts in other invaded areas, it is important to understand whether native prey could have naiveté to this potentially novel predator. Therefore, we tested whether native prey recognized the non-native peacock bass (*C. kelberi*) and its chemical cues, and compared their antipredator response to that with a native predator.

Materials and methods

We studied predator recognition by native prey using *Hemigrammus marginatus* Ellis (Characidae; SL = 36.7 ± 1.3 mm), a common macrophyte-associated species (Casatti et al. 2003), which had greatly declined after the peacock bass introduction (Pelicice and Agostinho 2009). *H. marginatus* is not known to co-occur with *Cichla* in its native range, although other members of this genus are native to the Amazon (e.g., Petry et al. 2003). A native piscivore, wolffish *H. malabaricus* Bloch (Erythrinidae) was used for the native predator treatment. *H. malabaricus* is an ambushing predator, most active during twilight hours (Frazer and Gilliam 1992). Two other prey species, *Apareidon affinis* Steindachner, Parodontidae and *Bryconamericus stramineus* Eigenmann, Characidae were used to confirm recognition of peacock bass but not the native predator due to insufficient number of individuals collected. Prey fish were collected by light traps and cast nets in lagoons or near-shore areas with littoral vegetation, whereas peacock bass and *Hoplias* were collected by angling in river and lagoon environments of the floodplain. All fish were collected in the region of the upper Paraná River floodplain located between Itaipu and Porto Primavera dams. Each species was housed in a separate holding tank with an independent water supply until the beginning of an experiment. Aquatic

plants were collected from channels and lagoons on the Paraná River. We created different structural habitats using *Eichhornia azurea*, a floating macrophyte with extensive underwater root system, which is the dominant native macrophyte in the floodplain (Bini et al. 2001) and *Hydrilla verticillata*, an invasive submerged macrophyte recently introduced in the Paraná River (Thomaz et al. 2009). Behavior was observed in a 1.5 by 1.2 m 1,000 l tank which was approximately half-full (∼40 cm deep) to provide optimal recording conditions. Three habitat types were provided in the observation tank: open water and two vegetated habitats, *Hydrilla* and *Eichhornia*. Vegetation was secured in place using wire, and positions of the two vegetated habitats were randomly alternated for different trials. We used a ∼40-stem cluster of *Hydrilla* and 3 or 4 60-cm stems of *Eichhornia*, containing a total of 12–15 nodes, of which 7–10 had dense root clumps. Preliminary recordings indicated that this was the greatest vegetation density achievable without compromising prey visibility to the observer, and similar vegetation density was found on the edge of a corresponding macrophyte bed (K. Kovalenko, personal observations). All experimental procedures were carried out at the NUPELIA station of Maringá State University located in Porto Rico, Paraná, Brazil.

In each trial, we used 20 prey fish to minimize stress and mimic small schools occurring under natural conditions (Casatti et al. 2003). Prey fish were placed in the observation tank and allowed to acclimate for at least 2 h. Preliminary observations indicated that this time was sufficient for fish to start behaving normally, i.e., swimming around the tank. After the acclimation period, prey behavior was recorded for 20 min prior to adding the chemical cue. Chemical cue (water from the predator holding tank) was added continuously by switching the intake of the flow-through system for the next 20-min period, during this time behavior was continuously recorded. After the chemical cue treatment, the actual predator was added to the tank and prey behavior was recorded for additional 20 min. Predators did not attack prey, possibly due to stressful conditions from handling and being in a light-colored tank. One predator was randomly assigned to each trial. One or two trials were done during a day, between 11am and 5 pm. Neither date nor time of day had any effect on any of the response variables (Mann–Whitney

$P > 0.05$). Trials were recorded using a digital movie camera (Xacti, VPC-C6, 6.0 Mp, Sanyo Electric Co., Osaka, Japan) placed above the observation tank and analyzed using a VLC media player.

Predator effects on prey behavior were assessed using the following variables recorded in situ (Table 1): (1) avoidance, defined as the number of times prey dashed away from the predator when the predator moved; (2) approach, as the number of times prey came close to either a moving or a non-moving predator; (3) habitat segregation, as the number of times predator and prey were observed in the opposite sides of the tank; and (4) prey habitat use, or proportion of time spent in each of the three habitats (open, *Hydrilla* and *Eicchornia*). Avoidance and approach behaviors were recorded using continuous behavior sampling, which is more suitable for analysis of discrete, rarely occurring behaviors (Martin and Bateson 1986), whereas habitat segregation and prey habitat use were recorded using scan sampling at 1 min intervals. Habitat use was compared only between control and chemical cue treatments but not the predator presence treatment because in the latter case prey habitat use reflected predator habitat use, since prey were avoiding the predator. Prey habitat use was quantified as number of times prey were observed in a given habitat divided by the total number of observations, and expressed as a difference between habitat use in control and predator chemical cue readings.

Prey activity and vigilant behavior in response to chemical cue or presence of peacock bass versus the native predator were analyzed from the recorded videos by randomly selecting five 30-s focal samples from each cue treatment (control, chemical and chemical + visual). Prey swimming activity was measured by counting number of lines crossed by overlaying a 5 × 5 cm grid over a computer monitor (corresponding to approximately 20 × 20 cm in the aquarium). In addition, prey exhibited distinctive vigilant or exploratory behavior, manifested in directionless movement, including zigzagging and turning around but did not involve approaching the predator (thereafter, zigzagging). This type of response was previously observed in other fish species in response to alarming stimuli (e.g., Pfeiffer 1977). Each instance of this behavior was quantified at the moment of an incomplete turn, after which another fish was selected and observed until this behavior was registered or up to 5 s. Prey fish were

Table 1 Behavioral variables recorded to assess predator recognition and predator effects on prey behavior, their definition and recording conditions

Prey behavior	Defined as	Recording method	Subject	Trial segment	Treatment
Avoidance	N times prey dashed away when predator moved	Continuous	Any fish, all occurrences	Actual predator presence (chem + visual)	Cichla vs. Hoplias
Approach	N times prey came close to a predator	Continuous	Any fish, all occurrences	Actual predator presence (chem + visual)	Cichla vs. Hoplias
Habitat segregation	N times predator and prey observed in opposite sides of tank	Scan sampling at 1 min intervals	Randomly selected fish	Actual predator presence (chem + visual)	Cichla vs. Hoplias
Habitat use	Proportion of counts in each of the three habitats	Scan sampling at 1 min intervals	Randomly selected fish	Control, chemical cue	Cichla vs. Hoplias
Swimming activity	N lines crossed	30 s Focal, video	Randomly selected fish	All	C. vs. H. by cue level
Vigilant/zigzagging	Directionless movement, turning around	30 s Focal, video	New fish selected after first turn or 5 s	All	C. vs. H. by cue level

not re-used in the course of the experiment to avoid habituation. We conducted a total of 10 trials (5 with native predator and 5 with Cichla); in two trials prey did not exhibit normal swimming activity in the control part of the experiment, so they were excluded from the analysis of prey activity, resulting in 4 native predator and 4 Cichla trials. Observation tank and all handling equipment were thoroughly washed and dried after each trial and aquatic plants were either replaced or rinsed for at least 30 min in running water in an effort to remove residual predatory cues.

Statistical analyses

Differences in avoidance and habitat segregation between the peacock bass and the native predator treatments were analyzed using the Mann–Whitney test. Prey did not approach predators except for a single case with peacock bass and a few instances with the native predator. Due to the incidental nature of this behavior, it was not analyzed. The chi-square test was used to determine significance of changes in prey habitat use within trials (using the Bonferroni correction for multiple tests, $\alpha < 0.005$) and the Mann–Whitney test was used to compare the difference in habitat use between the two predator treatments. Prey activity and vigilant behavior in response to the two predator treatments were analyzed using mixed model analysis of variance (SAS 9.1). For this analysis, predator type (native vs. invasive) was used as a fixed effect and the cue type (control, chemical and chemical + visual) as a repeated measure within each trial. Model fit was not improved by the addition of trial as a random variable; therefore, it was omitted from the final analysis. Residuals were normally distributed (Shapiro–Wilk $P > 0.05$). Compound symmetry was selected as the most appropriate covariance structure based on the AICc.

Results

Every time the predator moved, *H. marginatus* displayed avoidance behavior by dashing or swimming away from the predator and trying to maximize the distance from the predator (Fig. 1). There was obvious habitat segregation: prey and predator were
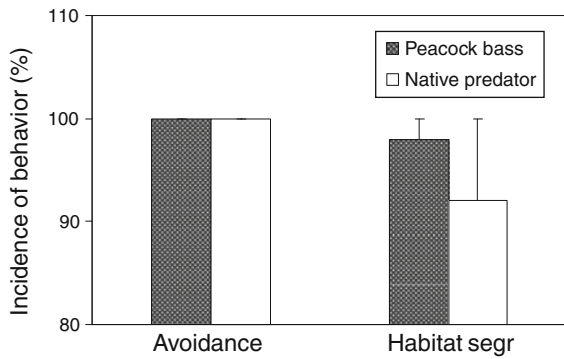
Fig. 1 Predator avoidance and habitat segregation in the presence of peacock bass (*dark*) versus native predator, *Hoplias*; $n = 10$, mean $\pm$ SE

Fig. 2 Change in prey habitat use in the presence of native predator (*Hoplias*) versus invasive peacock bass; $n = 10$, mean $\pm$ SE. Prey habitat use was counted as number of times prey were observed in a given habitat divided by the total number of observations. *Negative values* indicate decreased use of a given habitat

observed in different habitats 95% of the time (Fig. 1) and the two predator treatments were not significantly different ($U = 14$, $P = 0.93$). After the predator moved, prey would dart away to the opposite side of the tank but avoid the area which the predator had just left. This behavior was confirmed with the other two prey species, which exhibited predator avoidance in 100 and 88%, and habitat segregation in 100 and 95% of cases for *A. affinis* and *B. stramineus*, respectively.

A significant change in prey habitat use in response to the predator chemical cue was observed only in 3 of the 10 trials ($\chi^2_{1,15} = 8.9 - 23.0$, $P < 0.005$; Table 2). The direction of change was not consistent among trials and there were no differences in prey habitat shift between the native and invasive predator treatments ($U = 8-9$, $P = 0.40-0.53$; Fig. 2).

Fig. 3 Prey activity in response to chemical cues and the actual presence of peacock bass and native predator ($n = 8$, mean $\pm$ SE). Means with the same letter are not significantly different

Table 2 Change in prey habitat use after addition of chemical cues of peacock bass, *Cichla* or the native predator (*Hoplias*)

Trial	1	2	3	4	5
Cichla					
$\chi^2_{1,15}$	1.26	1.05	0.24	8.89	1.18
P value	0.53	0.59	0.89	**0.003**	0.55
Direction				<E/>O	
Hoplias					
$\chi^2_{1,15}$	13.54	5.58	6.14	4.62	23.00
P value	**0.001**	0.06	0.013*	0.1	**<0.0001**
Direction	<H/>O				<O/>H

* NS after Bonferroni correction for multiple tests. For direction of change: *O* open, *H* Hydrilla, *E* Eichhornia

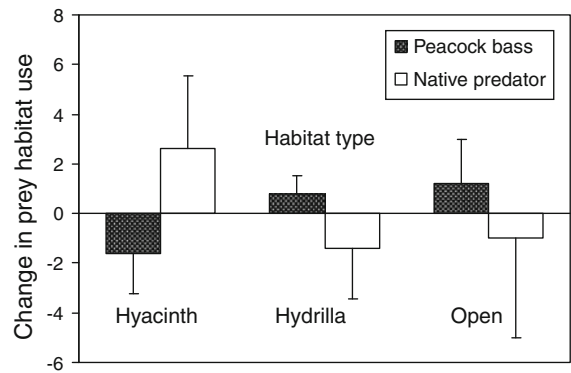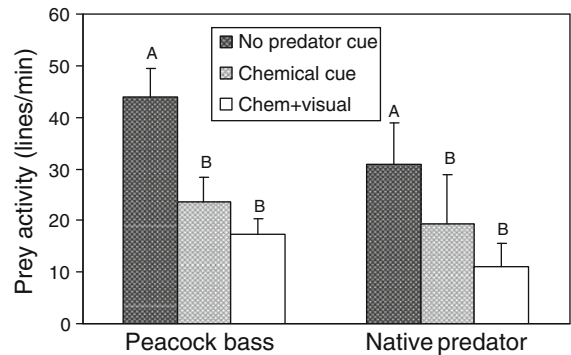*Note*: Significant *P* values in bold

Prey activity was significantly different with respect to the cue type (ANOVA $F_{3,8} = 30.82$, $P = 0.0005$; Fig. 3), whereas there was no significant difference between the two predators ($F_{2,8} = 0.93$, $P = 0.37$) and no interaction between the two factors ($F_{2,8} = 1.22$, $P = 0.35$). Prey activity decreased by an average of 45% in the presence of a chemical cue compared with the control and was not significantly different in the presence of a chemical cue versus the actual predator. This response was observed in as little as 30 s after the introduction of the cue and did not decrease in strength throughout the 20-min recording. Vigilant or zigzagging behavior was virtually absent in control recordings but became very conspicuous with the introduction of the cue (Fig. 4). There was a
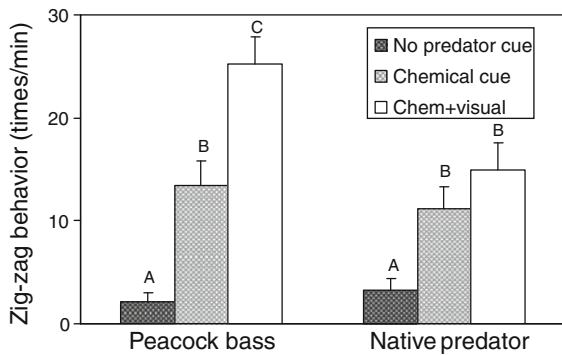
Fig. 4 Prey vigilant behavior (i.e., zigzagging) in response to chemical cues and the actual presence of peacock bass and native predator ($n = 8$, mean $\pm$ SE). Means with the same letter are not significantly different

significant interaction between the type of cue and predator ($F_{2,8} = 6.67$, $P = 0.025$; Table 3). Vigilant behavior increased by ~ 6.6-fold in response to the chemical cue ($F_{2,8} = 64.61$, $P < 0.005$), regardless of the predator type (no difference between predators, see Table 3 for effects slices). This behavior further increased by 2.2-fold in the presence of an actual predator in the case of peacock bass ($P < 0.0003$) but not the native predator ($P = 0.11$).

Discussion

Our data clearly show that non-native peacock bass is recognized as a predator and avoided as much or more than the native piscivore *Hoplias*. This type of behavior was not elicited by a similar-sized non-predatory cyprinid (unpublished data), indicating that it was in fact an antipredator response rather than general avoidance of a large moving object. Spatial avoidance, decreased activity and increased vigilant behavior observed in this study are among the most common antipredator responses (e.g., Lima and Dill 1990 and references therein; Gerlai 1993; Lautala and Hirvonen 2008). Decreased activity reduces the likelihood of detection by the predator, whereas increased vigilant behavior allows adequate assessment of predation risk. We did not observe marked additivity of chemical and visual cues, except for zigzagging behavior in response to the peacock bass. It is only natural for the prey to display a near-maximum reaction to the chemical cue, as it is critical to detect predators before being detected. In this case, adding visual cues did not present any new information, although a different response may be expected with a foraging predator. Smith and Belk (2001) found that chemical cues had greater effects on prey behavior than the visual cue of predator size and observed an additive response for one of the three types of behavior examined. Prey did not approach predators in our study, possibly because they could correctly assess the level of risk, since prey are reluctant to approach more dangerous predators (Dugatkin and Godin 1992).

Another common antipredator response is a shift in habitat use, most often manifested in the increased

Table 3 Effects of the cue (control, chemical, chemical + visual) and predator type (*Cichla* vs. *Hoplias*) on prey zigzagging behavior

Effect	numDF	denDF	F	P
Cue	2	6.82	64.61	**<0.001**
Pred	1	6.08	2.63	0.155
Cue × pred	2	6.82	6.67	0.025

Predator	Cue type	P	Direction of effect
Cichla	Control vs. chemical cue	**0.001**	Increased compared to control
Hoplias	Control vs. chemical cue	**0.005**	Increased compared to control
Cichla	Chemical vs. actual predator	**<0.001**	Increased with actual predator
Hoplias	Chemical vs. actual predator	0.112	NA
Cichla vs. Hoplias	Chemical	0.503	NA
Cichla vs. Hoplias	Actual predator (visual/chem)	**0.027**	Greater in Cichla

Structure of the ANOVA table and *P* values associated with effect slices for comparisons of interest

Note: Significant *P* values in bold

use of vegetated habitats (e.g., Sih 1987; Stuart-Smith et al. 2008). In our study, prey did not increase their use of vegetation in the presence of predatory cues. It is possible that prey were unable to localize the predator based on chemical cues alone. There is also a possibility that plant density presented in this experiment was insufficient to be perceived by the prey as a refuge and was not utilized to minimize visual interference and improve predator detection. In fact, experiments carried out in lakes connected to the Paraná River showed a great concentration of small-sized fish inside *E. azurea* stands, suggesting that macrophytes are used as refuge (Agostinho et al. 2007). Gotceitas and Colgan (1987) demonstrated that bluegills were able to select vegetated habitats which would offer them optimal protection and avoided cover plots with the lowest vegetation density. It is also possible that prey are capable of differential response to different types of predators (e.g., Keefe 1992; Hirvonen et al. 2000) and since in this case both predators are often associated with macrophytes, vegetation may be perceived as a more dangerous habitat. This provides additional support for the indirect evidence indicating that macrophytes play a very limited role in minimizing impacts of this introduced predator (Latini and Petrere 2004; Pelicice and Agostinho 2009).

Several previous studies demonstrated that prey may have limited recognition of non-native or unfamiliar predators. For example, tadpoles of *Bufo americanus* and *Rana catesbeiana* did not change activity level and habitat use in response to cues from a non-native predator (Smith et al. 2008). New Zealand crayfish (*Paranephrops zealandicus*) were unable to recognize chemical cues of the invasive brown trout despite the fact that 120 years had passed since the trout was introduced (Shave et al. 1994). There are often population-level differences in predator recognition, and only the individuals from populations sympatric with the predator recognize predatory cues whereas those from allopatric populations do not (Gerlai 1993; Mathis et al. 1993; Kiesecker and Blaustein 1997). However, there is evidence that some prey may recognize predators without prior exposure. Invasive predators are known to induce habitat shifts in native prey (*Galaxias auratus*, Stuart-Smith et al. 2008; *Iotichthys phlegethontis*, Mills et al. 2004). Whitlow et al. (2003) reported that soft-shell clams responded to introduced

green crabs by burrowing deeper into the sediment. Invasion of a Trinidad stream by *Hoplias malabaricus* altered habitat use by native fish (Frazer and Gilliam 1992). Prey recognition of previously unfamiliar predators can be either innate or learned. There is some innate capacity for general antipredator responses such as fleeing from an overhead shadow (Giles 1984) or a large moving object (Magurran 1990). An innate response may be related to the species' co-evolutionary history with predators, as evidenced by the very different antipredator responses to an unfamiliar predator in two sympatric and morphologically similar species which experienced different predation pressure during their evolutionary history (Nannini and Belk 2006). However, in most cases learned recognition is more important than innate responses (Chivers and Smith 1994), as it allows for more plastic and threat-sensitive behavior (Brown and Chivers 2005). Prey can learn to recognize previously unfamiliar predators by detecting a conspecifics' alarm signature in a predator's diet (Mathis and Smith 1993b; Brown and Godin 1999). However, presence of prey alarm cues in our study was unlikely, as most predators used in the experiment were not feeding due to restricted conditions and were not offered food before the experiment. Alternatively, since prey were collected from the wild, it is possible that they have previously encountered peacock bass (despite the fact that their population density is still relatively low, Agostinho et al. 2004) and associated it with damaged conspecifics. Regardless of the origin of predator recognition observed in this study, it means that *Cichla* impacts are not due to prey naiveté, therefore, prey learning is unlikely to contribute to the decrease in mortality and leveling off in the rate of extinctions in the future. It also means that even systems without prey naiveté may experience deleterious effects from this invasion.

Predator recognition is an essential part of an antipredator response but it is not the only factor that ultimately determines prey survival. Prey could recognize predators but not display an appropriate behavior or simply be 'outgunned' by the predator's hunting technique (Banks and Dickman 2007). It might be difficult to experimentally distinguish between these two possibilities, not least because they rely on an untestable assumption of what the appropriate behavior might be. Sometimes the

expected "optimal" antipredator strategy does not result in lower mortality (Nannini and Belk 2006; Rehage et al. 2009).

The likelihood of developing a successful antipredator strategy to a non-native predator will depend on prey behavioral plasticity, length of time since the evolutionary separation, and the strength of predator effect. In this case, native prey were exposed to relatively high predation pressure and have probably retained behavioral plasticity and some basis for recognition of unfamiliar predators despite a relatively long separation from this invasive predator. Yet, in order for selection process to operate, there needs to be differential survival of prey, and considering nearly a complete assemblage extermination in just 2 years after the peacock bass invasion (as shown by Pelicice and Agostinho 2009), it seems unlikely that native fish would have the opportunity to develop an effective antipredator strategy.

It is interesting that peacock bass was suggested to be playing a role in maintaining species diversity in its native range (Jepsen et al. 1997), but was reported to cause species extinctions and extirpations in its introduced range (Zaret and Paine 1973; Latini and Petrere 2004; Pelicice and Agostinho 2009). It is possible that peacock bass has less of an impact on the resident species in its native range because a large proportion of its energy budget comes from the seasonal migrations of prochilodontids (Jepsen et al. 1997; Hoeinghaus et al. 2006). In the Paraná River, these migrations were negatively affected by dams (Gubiani et al. 2007), thereby forcing peacock bass to rely on small characids, which are possibly a suboptimal food source for these large predators. In fact, peacock bass introductions are often unsuccessful in the longer term, as they deplete local prey and resort to cannibalism (Santos et al. 1994; Gomiero and Braga 2004; Fugi et al. 2008). Alternatively, the dramatic effects of peacock bass on native fish could be due to the absence of effective refugia from predation, either spatial or temporal. Fish assemblages in this part of the Paraná River were regulated by predation even in the absence of peacock bass (Piana et al. 2006). However, persistence of this system may have depended on the presence of environmental heterogeneity in the form of floods, which provided seasonal protection to prey populations. Therefore, observed extinctions may be due to a *community-level naiveté* to this type of predatory

regulation in the absence of temporal refugia provided by floods, which greatly decreased in magnitude after the creation of dams. Indeed, variation in hydrology allowing a seasonal release from predation during high-water periods may be responsible for the successful co-existence of many species with peacock bass in its native range (Jepsen et al. 1997). It is important to test these hypotheses in order to understand the mechanisms responsible for peacock bass impacts and use this knowledge to design refugia to protect native species.

In conclusion, our study shows that native prey recognize and avoid a non-native predator, *Cichla kelberi*, and respond to its chemical cues by decreasing activity and increasing vigilant behavior. These antipredator responses were similar to those observed with a native predator, *H. malabaricus*. The main implications of this study are that the rate of extinctions is unlikely to level off in the future as a result of prey learning and, secondly, that even systems with high native diversity and absence of prey naiveté may be vulnerable to extinctions after the introduction of an exotic predator.

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