

Aggressive interactions between the invasive Rio Grande cichlid (*Herichthys cyanoguttatus*) and native bluegill (*Lepomis macrochirus*), with notes on redspotted sunfish (*Lepomis miniatus*)

O. Thomas Lorenz · Martin T. O'Connell ·
Pamela J. Schofield

Received: 26 April 2009 / Accepted: 21 April 2010
© Japan Ethological Society and Springer 2010

Abstract The Rio Grande cichlid (*Herichthys cyanoguttatus*) has been established in the Greater New Orleans Metropolitan area for at least 20 years, and its effect on native fishes is unknown. Behavioral trials were performed to determine if aggressive interactions occur between invasive *H. cyanoguttatus* and native bluegill (*Lepomis macrochirus*). When defending a territory as the resident, *L. macrochirus* were markedly aggressive, averaging 11.6 aggressive actions per 10-min behavioral trial. In contrast, *L. macrochirus* were extremely passive as invaders, with 0.5 aggressive actions per trial. *Herichthys cyanoguttatus* were equally aggressive as residents and as invaders, averaging 4.9 and 6.0 aggressive actions per trial, respectively. *Herichthys cyanoguttatus* interacted aggressively with native species whether they held territory or not, indicating that this invasive species may have fundamentally different strategies of aggression compared with native *L. macrochirus*. These differences may explain the continued success of *H. cyanoguttatus* as an invasive fish in southeastern Louisiana.

Keywords Aggression · Centrarchid · Cichlid
invasive · Residence

O. T. Lorenz (✉) · M. T. O'Connell
Pontchartrain Institute for Environmental Sciences,
University of New Orleans, New Orleans LA70148, USA
e-mail: otlorenz3@yahoo.com

P. J. Schofield
US Geological Survey, Southeast Ecological Science Center,
7920 NW 71st Street, Gainesville, FL 32653, USA

Introduction

Invasive species pose a significant threat to native organisms (Vitousek et al. 1997), and the number of non-native species that are discovered continues to increase (Crossman 1991; Fuller et al. 1999). For example, the Rio Grande cichlid (*Herichthys cyanoguttatus*) has been established in natural habitats and canals of the Greater New Orleans Metropolitan Area (GNOMA) for 20–30 years (Fuentes and Cashner 2002; O'Connell et al. 2002). This species is native to the southern drainages of the Rio Grande River with its type locality being Brownsville, Texas (Baird and Girard 1854). Populations in the United States were once restricted to the southern half of the Rio Grande River basin, but now *H. cyanoguttatus* occurs in many parts of Texas, including the Guadalupe River basin, the San Antonio area, and the Edwards Plateau region (Brown 1953; Hubbs et al. 1978; Fuller et al. 1999). Outside Texas, the only established populations in the United States are in Florida and Louisiana (Fuller et al. 1999).

The potential threat of *H. cyanoguttatus* to native fauna is unclear. It appears to compete for breeding sites with native centrarchids such as bluegill (*Lepomis macrochirus*) in Florida (Courtenay et al. 1974), and we have observed aggressive interactions between these species in Louisiana. Our unpublished field observations have revealed that *H. cyanoguttatus* also acts aggressively toward native largemouth bass (*Micropterus salmoides*), western mosquitofish (*Gambusia affinis*), sailfin molly (*Poecilia latipinna*), and blue crab (*Callinectes sapidus*). This type of aggression by invasive species can inhibit growth and reproduction as well as shift habitat use of native species (Marchetti 1999; Schrank et al. 2003).

In this study, we observed interactions between invasive *H. cyanoguttatus* and native *L. macrochirus* under

laboratory conditions to determine what levels of aggression were exhibited by different species in different contexts (invader or resident). We also conducted similar observations (though with fewer trials) on interactions between *H. cyanoguttatus* and native redspotted sunfish (*L. miniatus*), a particularly aggressive native centrarchid (personal observation). In general, most species of the families Cichlidae and Centrarchidae are considered aggressive freshwater fishes, with members of both groups employing aggression in interspecific and intraspecific interactions (Marchetti 1999; Matsumoto and Kohda 2004). Intraspecific behavioral studies have shown that *H. cyanoguttatus* are aggressive as invaders and as residents (Turner 1994; Draud et al. 2004; Leiser et al. 2004), and that *L. macrochirus* are aggressive as territory-holding adult males (Colgan et al. 1978). Relatively few studies have examined interspecific aggression within these families (Colgan and Gross 1977; Matsumoto and Kohda 2004), and cichlid–centrarchid interactions have only rarely been studied (e.g., Brooks and Jordan 2009). Such a study could demonstrate behavioral effects of invasive species and better explain success of non-native fishes in the wild. Therefore, we conducted behavioral trials in aquaria to determine what aggressive strategies are exhibited by *H. cyanoguttatus*, *L. macrochirus*, and *L. miniatus* during interspecific interactions.

Materials and methods

Most fishes used in the trials (86 *H. cyanoguttatus*, 80 *L. macrochirus*, and 6 *L. miniatus*) were collected from canals and bayous in the GNOMA from January to August 2007 using electrofishing, seining, and trapping. Additional *L. macrochirus* were obtained from a local hatchery to supplement the number of wild-caught fish. It is possible that hatchery *L. macrochirus* had differences in behavior from wild-caught *L. macrochirus* but this was not measured here. Approximately half of all *L. macrochirus* were from the local hatchery. All *H. cyanoguttatus* and *L. macrochirus* were juveniles (range 40–100 mm SL) and were given at least a week to acclimate to laboratory conditions. The six *L. miniatus* (range 90–130 mm SL) may have been large enough to be adults (Ross 2001). Species were maintained separately in 400-l aquaria prior to trials. All fishes were fed ad libitum with commercial fish food and aquaria were filtered by air-driven sponge filters. Water conditions were measured before each trial. Temperature was kept at 24.5°C and never varied more than 0.5°C, pH remained constant at 7.5 for every trial. No mortalities occurred during these trials. *Herichthys cyanoguttatus*, *Lepomis macrochirus*, and *L. miniatus* were either kept for other experiments (not related to behavior) or sacrificed by freezing after the trials.

Lepomis miniatus were donated to a local aquarium for a native species display.

Behavioral trials were conducted in 75-l aquaria containing gravel substrate and an air-driven sponge filter. Based on similar behavioral trials (Wazlavsek and Figler 1989; Ratnasabapathi et al. 1992; Glova 2003; Metcalfe et al. 2003), one fish was introduced into the experimental aquaria and allowed 24 h to acclimate to either a clay pot or a portion of PVC pipe (the “territory”). After 24 h of residence, an opaque divider was inserted into the middle of the aquarium and a fish of similar size but different species was introduced to the opposite side. This “invader” was also provided with a temporary territory upon introduction to the aquarium to reduce handling stress. After 10 min, the temporary territory and divider were removed and all interactions were videotaped for 10 min. To minimize observer effects, no humans were in the room during videotaping. After each trial, both fishes were removed with a net, measured to the nearest mm standard length (SL), and weighed to the nearest g. Individual fish were used only once during these behavioral trials. Forty trials were conducted with *L. macrochirus* as the resident and *H. cyanoguttatus* as the invader, with 20 trials having a *H. cyanoguttatus* larger than the resident and 20 trials having a *H. cyanoguttatus* smaller than the resident. No invading fish were more than twice or less than half the size of the resident. This approach was repeated for another 40 trials with a *H. cyanoguttatus* as the resident and a *L. macrochirus* as the invader.

A similar approach was taken to observe *H. cyanoguttatus*–*L. miniatus* interactions, though only six total trials were conducted due to a lack of available *L. miniatus*. All trials involved *L. miniatus* as the resident. As with the other trials, half (3) of the trials involved a *H. cyanoguttatus* smaller than the resident and half involved a *H. cyanoguttatus* larger than the resident. For these six trials, both sets of *H. cyanoguttatus* and *L. miniatus* were larger adult fish (range 90–130 mm SL).

From the videotape, we recorded the number and type of aggressive behaviors exhibited by the fishes. Specifically, we counted the number of:

1. lunges (a fish moving toward its opponent with flared opercula);
2. lateral displays (a fish turning its body sideways to its opponent with fins spread and usually undulating);
3. chase/bites (an escalated behavior when a fish either intends injury by chasing or actually inflicts injury with a bite).

This is a rough order of how cichlids sequentially assess one another in contests (Enquist et al. 1990). These behaviors were then summed together to obtain ‘total aggressive behavior’ counts for each fish. If a fish repeated

the same behavior multiple times without any behavioral interaction from the opponent (e.g., several consecutive lunges), the behavior was only counted once. Unfortunately, it was unclear which fish owned the territory at the end of most trials (no obvious “victor”).

We used three-way ANOVA to analyze aggression data, with the main effects of size (larger or smaller), residence (resident or invader), and species (*L. macrochirus* or *H. cyanoguttatus*). Homogeneity of variances was assessed with Levene’s test. To determine whether datasets met the assumption of normality, histograms and normal P–P plots of residuals were visually inspected. Additionally, multicollinearity (i.e., correlation of variables) was tested with Durbin–Watson statistic (accepted if 1.0–3.0). Square-root (+1) transformations were used to normalize the distributions of three response variables (‘lunge’, ‘display’, and total aggression). We were unable to transform the response variable ‘chase’ such that its distribution met our standards of normality, and therefore did not perform statistical analysis on this variable. When both main effects and interactions were significant, we compared their relative strengths with partial eta-squared scores. When partial eta-squared scores for the interaction were greater than the main effects, only the interaction term(s) was/were discussed.

To analyze significant interactions, we compared the four separate distributions (every combination of the two

main effects) with one-way ANOVA. Levene’s test was used to determine whether variances were heterogeneous, and when they were, we used Dunnett’s T3 test for post hoc analysis. To take into account the fact that we performed multiple tests on the same dataset, we set our acceptable level for significance as $P < 0.01$.

For *L. miniatus* trials, residence was always the same (‘invader’ for *H. cyanoguttatus* and ‘resident’ for *L. miniatus*). Thus, a two-way ANOVA was performed examining the effects of species (*H. cyanoguttatus* vs *L. miniatus*) and size (larger or smaller) on the total number of aggressive acts. The data were tested for normality and homogeneity of variances as above (for *L. macrochirus*) and it was determined that no transformation was needed. Because the number of trials was small, the four subsets (species × size combinations) were not compared. All analyses were carried out using SPSS v. 12.0.

Results

Results from the three-way ANOVA analyses of aggressive behaviors between *H. cyanoguttatus* and *L. macrochirus* showed that the interaction of species and ownership was the most significant variable (Table 1). Partial eta-squared scores for the interaction term (species × ownership; Table 1) were generally greater than either of the two main

Table 1 ANOVA tables for: total aggression, displays and lunges for *H. cyanoguttatus* versus *L. macrochirus* interactions and total aggression for *H. cyanoguttatus* versus *L. miniatus* interactions

Source	Type III sum of squares	df	Mean square	F	P	Partial eta-squared
<i>H. cyanoguttatus</i> versus <i>L. macrochirus</i> interactions						
Total aggression						
Corrected model	102.29	7	14.61	16.89	0.000	0.437
Intercept	848.16	1	848.16	980.05	0.000	0.866
Species	1.12	1	1.12	1.29	0.258	0.008
Size	2.99	1	2.99	3.45	0.065	0.022
Owner	35.76	1	35.76	41.32	0.000	0.214
Species × size	1.23	1	1.23	1.42	0.235	0.009
Species × owner	54.55	1	54.55	63.04	0.000	0.293
Size × owner	0.58	1	0.58	0.67	0.415	0.004
Species × size × owner	6.07	1	6.07	7.01	0.009	0.044
Error	131.55	152	0.87			
Total	1,082.00	160				
Corrected total	233.84	159				
Displays						
Corrected model	58.50	7	8.36	20.94	0.000	0.491
Intercept	365.84	1	365.84	916.77	0.000	0.858
Species	17.11	1	17.11	42.87	0.000	0.220
Size	0.66	1	0.66	1.66	0.200	0.011
Owner	13.18	1	13.18	33.02	0.000	0.178

Table 1 continued

Source	Type III sum of squares	df	Mean square	F	P	Partial eta-squared
Species × size	0.02	1	0.02	0.06	0.814	0.000
Species × owner	27.21	1	27.21	68.19	0.000	0.310
Size × owner	0.28	1	0.28	0.69	0.406	0.005
Species × size × owner	0.04	1	0.04	0.10	0.747	0.001
Error	60.66	152	0.40			
Total	485.00	160				
Corrected total	119.16	159				
Lunges						
Corrected model	44.40	7	6.34	14.03	0.000	0.393
Intercept	556.89	1	556.89	1231.96	0.000	0.890
Species	22.89	1	22.89	50.64	0.000	0.250
Size	0.27	1	0.27	0.60	0.441	0.004
Owner	6.20	1	6.20	13.73	0.000	0.083
Species × size	0.27	1	0.27	0.60	0.439	0.004
Species × owner	10.76	1	10.76	23.81	0.000	0.135
Size × owner	0.78	1	0.78	1.73	0.191	0.011
Species × size × owner	3.22	1	3.22	7.12	0.008	0.045
Error	68.71	152	0.45			
Total	670.00	160				
Corrected total	113.11	159				
<i>H. cyanoguttatus</i> versus <i>L. miniauts</i> interactions						
Total aggression						
Corrected model	909.45	3	303.15	6.42	0.006	0.579
Intercept	4,779.49	1	4,779.49	101.22	0.000	0.878
Species	530.53	1	530.53	11.24	0.005	0.445
Size	0.08	1	0.08	0.00	0.967	0.000
Species × size	320.53	1	320.53	6.79	0.021	0.327
Error	661.05	14	47.22			
Total	6,471.00	18				
Corrected total	1,570.50	17				

See text for details of analyses

effects (species and ownership); therefore, we discuss the implications of the interaction relative to the behavior (and not the main effects). This pattern was apparent for total aggression, lunges, and displays (Table 1a–c). Total aggressive behaviors (lunges + displays + chases) for *H. cyanoguttatus* did not differ in response to its resident versus invader status; however, *L. macrochirus* was more aggressive than *H. cyanoguttatus* when a resident and less aggressive than *H. cyanoguttatus* when an invader (Fig. 1). Resident *L. macrochirus* were more likely to perform lunges and displays than invading *L. macrochirus* or *H. cyanoguttatus* (resident or invader; Figs. 2 and 3).

Lepomis miniatus was more aggressive than *H. cyanoguttatus*, and this was especially true when the *L. miniatus* individuals were larger than their *H. cyanoguttatus* tank mates (Table 1d; Fig. 4).

Discussion

Non-native *H. cyanoguttatus* showed consistent levels of aggression as intruders and as residents, whereas native *L. macrochirus* had the highest overall levels of aggression (but only as residents). Native *L. miniatus* were also aggressive residents. These data show *H. cyanoguttatus* to be aggressive towards centrarchids in two different contexts (as resident and invader). The difference in behaviors between the species could indicate distinct game theory strategies; non-native *H. cyanoguttatus* appear ‘hawk-like’ (sensu Maynard Smith 1974, 1982) because it is aggressive in all encounters, native *L. macrochirus* appear to be ‘hawk-like’ while defending territory and ‘dove-like’ while invading territory. This would categorize *L. macrochirus* as ‘bourgeois-like’ (Maynard Smith 1974, 1982). The actual

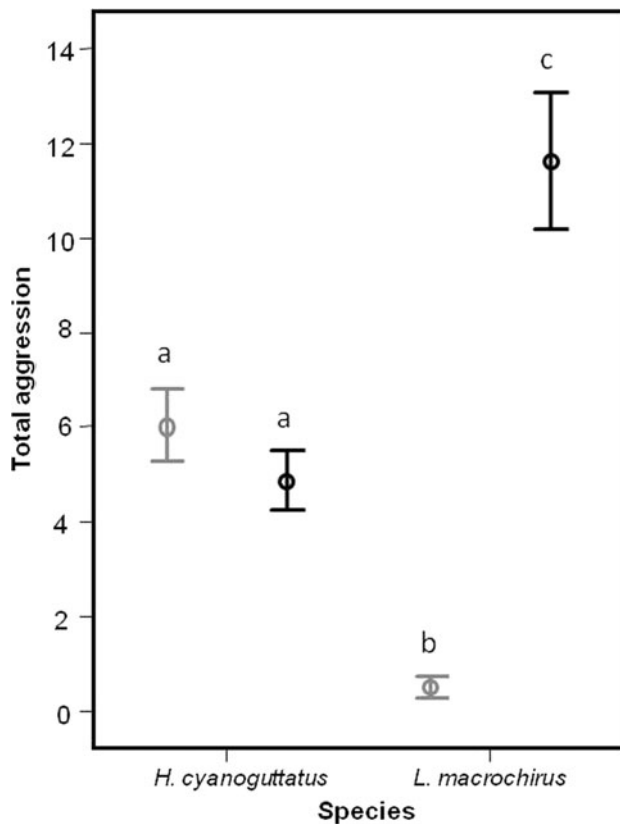


Fig. 1 Mean (± 1 SE) number of total aggressive acts of *H. cyanoguttatus* and *L. macrochirus*. Gray bars aggressive acts when fish were invaders; black bars resident fishes. See text for details of data collection and how aggressive acts were scored and counted. Letters above each value denote significantly different subsets (one-way ANOVA with Dunnett's T3 post hoc; $P < 0.01$)

game theory strategies of these species can only be discovered by examining the costs of fighting and the benefits of holding these territories. In a separate study with paired *L. macrochirus* and *H. cyanoguttatus*, Lorenz and O'Connell (2008) noted reduced growth of *H. cyanoguttatus* that were larger than their *L. macrochirus* counterparts, compared to smaller (and presumably non-dominant) *H. cyanoguttatus*. It is possible that the costs of holding a territory limited the growth of the dominant individuals. These fish were introduced at the same time and were kept in large pools, so residence and actual interactions were not measured. Further study of territory costs in these species could be done with closer observations of growth and dominance.

Brooks and Jordan (2009) found resident tilapia (*Tilapia mariae*) to be more aggressive residents than centrarchids. Using a mix of centrarchid species, they also had the unusual result of neither tilapia nor centrarchid being aggressive as intruders. This contrasts with this study where *H. cyanoguttatus* is aggressive as both an intruder and as a resident, and where *L. macrochirus* and

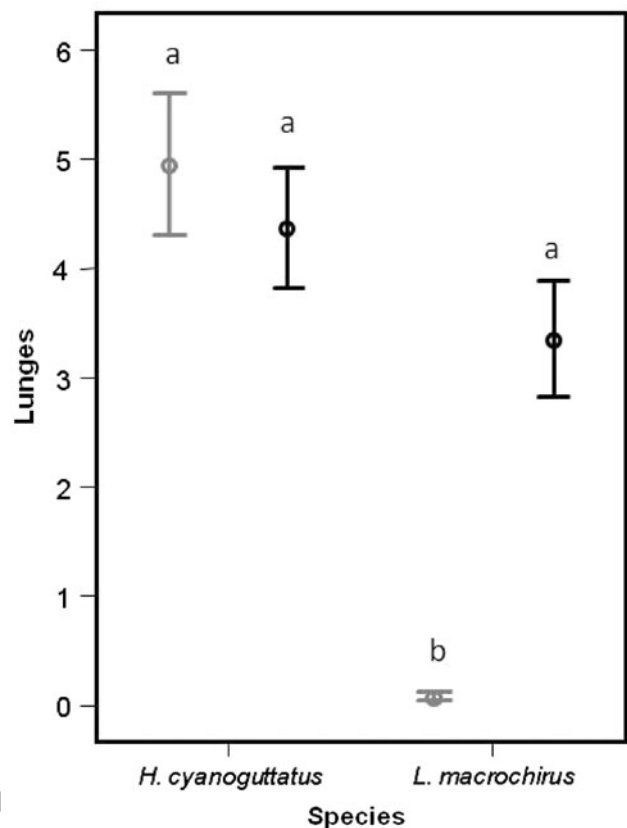


Fig. 2 Mean (± 1 SE) number of lunges of *H. cyanoguttatus* and *L. macrochirus*. Gray bars aggressive acts when fish were invaders; black bars resident fishes. See text for details of data collection and how aggressive acts were scored and counted. Letters above each value denote significantly different subsets (one-way ANOVA with Dunnett's T3 post hoc; $P < 0.01$)

L. miniatus are much more aggressive as residents. It is possible that the long residence time used (3 days) or the small aquaria (18 l) affected the results in their study, but it is hard to explain the lack of aggression of resident centrarchids, especially considering the lack of aggression of invading tilapia in those pairings.

Fishes use different behaviors to communicate different levels of aggression when there is a contest over a territory (Enquist et al. 1990), and these different behaviors were also apparent with these contests. No sequential data were recorded, but lateral displays and lunges were used before chasing and biting. Lateral displays are the most common display for *L. macrochirus* and lunges are the most common display for *H. cyanoguttatus*. There was a nonsignificant increase of lateral displays for larger *H. cyanoguttatus*. This may indicate the desire of *H. cyanoguttatus* to communicate its advantage in size to prevent any damaging combat and has been recorded in other cichlids, especially early in contests (Enquist et al. 1990). Escalated behavior, chasing and biting, was most common with *L. macrochirus* that were defending a territory. This indicates the perceived value of

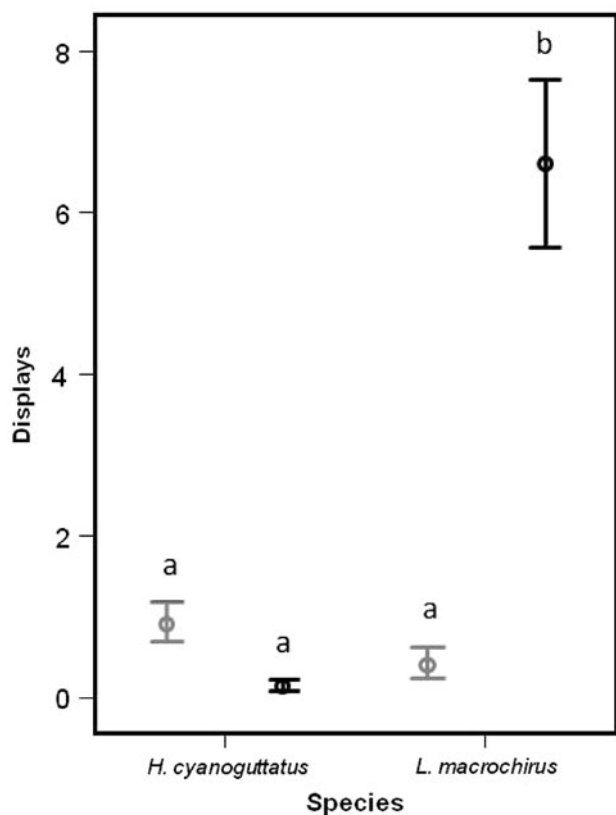


Fig. 3 Mean (± 1 SE) number of displays of *H. cyanoguttatus* and *L. macrochirus*. *Gray bars* aggressive acts when fish were invaders; *black bars* resident fishes. See text for details of data collection and how aggressive acts were scored and counted. *Letters* above each value denote significantly different subsets (one-way ANOVA with Dunnett's T3 post hoc; $P < 0.01$)

the territory for resident *L. macrochirus*, which were willing to risk injury by engaging in costly behavior. The interspecies communication of sequential assessment only seemed to break down at the occasional attempt by *H. cyanoguttatus* to 'mouth wrestle', which is a common aggressive behavior in cichlids (Draud and Lynch 2002). The native *L. macrochirus* did not engage in this behavior and turned away from such challenges. Interestingly, *L. miniatus* chose to bite *H. cyanoguttatus* that attempted to mouth wrestle.

Other aspects may affect behavior between two species. Size of territories is relevant. Convict cichlids (*Archocentrus nigrofasciatus*) have a cost associated with increasing territory size (Breau and Grant 2002). In conjunction with territory size, fish density will also be important. In the GNOMA canals, *H. cyanoguttatus* live in very high densities and the combination of this with their 'hawk-like' behavior may be significant. There is also the issue of multiple species interactions, including new strategies, such as a 'sneaker' stealing the resource (Dubois et al. 2004), which could exploit the "aggressive neglect" of hawk strategies (Wilson 1975). Large schools of fish can

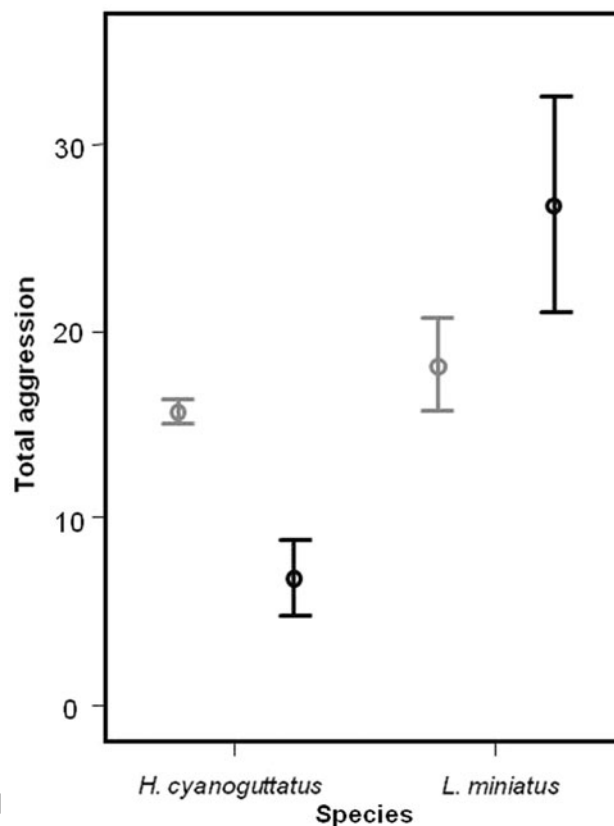


Fig. 4 Mean (± 1 SE) number of total aggressive acts of *H. cyanoguttatus* and *L. miniatus*. *Gray bars* aggressive acts when fish were smaller than the other species; *black bars* fish that were larger than the other species. See text for details of data collection and how aggressive acts were scored and counted. Because the number of trials was small, the four subsets (species \times size combinations) were not compared

also overwhelm territorial fish as seen in the "St. Ignatius effect" (Barlow 1974). In addition to prior residence, there are other important variables. Size is important in determining the outcome of contests in cichlids (Barlow et al. 1986; Wazlavsek and Figler 1989; Keeley and Grant 1993; Turner 1994). Temperature would also be a potential factor, especially with the tropical cichlids (Ratnasabapathi et al. 1992). Introduced eastern mosquitofish (*Gambusia holbrooki*) showed less aggression towards native Spanish toothcarps (*Aphanius iberus* and *Valencia hispanica*) when temperatures were lower (Rincon et al. 2002).

The aggression of juvenile fish in the present study suggests that territoriality is not just restricted to breeding adults, though strategies are known to change in fishes when they become larger and more capable of inflicting damage (Leiser et al. 2004). It also suggests that the territory being defended is more likely associated with increased food resources or protection from predators. The convict cichlid will defend predictable resources of food (Grand and Grant 1994). However, both *H. cyanoguttatus*

and *L. macrochirus* have generalist feeding strategies and *L. macrochirus* leaves a food patch when food resources are plentiful (Wildhaber et al. 1994), indicating that food patches are not a critical item for them to defend. Studies of aggressive behavior under different levels of predation pressure and cover could demonstrate the relative importance of these variables to individual species.

Aggression of *H. cyanoguttatus* in these trials may play a role in affecting native fishes, especially since similar aggression has been observed in the field (Courtenay et al. 1974; personal observation). Our results suggest a more specific explanation as to why *H. cyanoguttatus* continues to expand its range in Louisiana. There is an energetic cost to aggression and these trials show that there is typically a contest of long duration between *H. cyanoguttatus* and *L. macrochirus* if the sizes are close, especially if *L. macrochirus* are the residents. This is a serious concern, because there are high densities of *H. cyanoguttatus* in the areas where it is found, and prior residence will not dissuade *H. cyanoguttatus* from aggressively interacting with native species. Invasive species that initiate aggressive encounters can displace native species, as has been seen with the invasive Argentine ant (*Linepithema humile*; Human and Gordon 1999). Other studies show effects of invasive species on natives via aggressive behavior (Gunckel et al. 2002; Warburton and Madden 2003; Klocker and Strayer 2004; Dame and Petren 2006). Like many invasive species, *H. cyanoguttatus* is most successful in disturbed habitats, including GNOMA (personal observation), and this could be due to a lack of complex interactions in the relatively low diversity of city canals. This invasive species appears to be displacing native species (O'Connell, unpublished data) and it is possible that this is due in part to competitive interactions. Lorenz (unpublished data) indicates that *H. cyanoguttatus* diet in GNOMA is varied, with some animal diet in more natural waterways and algae in canal systems, which may also be relevant to competitive interactions. Much of this must be viewed as speculative, and more work still needs to be done to learn more about costs and benefits of these strategies in laboratory and field conditions. Further examination of behavioral interactions between native and non-native species can help resource managers identify species that pose the greatest threat to native communities.

Acknowledgments This research was supported by a Louisiana Board of Regents Graduate Student Fellowship and by a scholarship from the Coastal Restoration and Enhancement through Science and Technology program (CREST). Fishes were collected under Louisiana Department of Wildlife and Fisheries Scientific Freshwater Collecting Permit # 64-2007 and handled in accordance with IACUC permit # UNO-171. We thank M.N. Taracena, J. Van Vrancken, C.S. Schieble, and A.M.U. O'Connell for help with fieldwork. J. Howard,

F. Jordan and D. Slone provided valuable advice on experimental design and data analyses. We also thank R.C. Cashner, J.M. King, and S.L. Penland for their continued encouragement and support of these endeavors. This manuscript represents publication No. 5 for the Nekton Research Laboratory, Pontchartrain Institute for Environmental Sciences.

References

- Baird S, Girard C (1854) Description of new species of fishes collected by John H. Clark on the V.S. and Mexican boundary survey, and in Texas, by Captain Stewart Vliet. *Proc Acad Nat Sci Philadelphia* 7:24–29
- Barlow G (1974) Extraspecific imposition of social grouping among surgeonfishes (Pisces: Acanthuridae). *J Zool* 174:333–340
- Barlow G, Rogers W, Fraley N (1986) Do Midas Cichlids win through prowess or daring? It depends. *Behav Ecol Sociobiol* 19:1–8
- Breau C, Grant JWR (2002) Manipulating territory size via vegetation structure: optimal size of area guarded by the convict cichlid. *Can J Zool* 80:376–380
- Brooks WR, Jordan RC (2009) Enhanced interspecific territoriality and the invasion success of the spotted tilapia (*Tilapia mariae*) in South Florida. *Biol Invasions*. doi: 10.1007/s10530-009-9507-3
- Brown W (1953) Introduced fish species of the Guadalupe River basin. *Tex J Sci* 5:245–251
- Colgan P, Gross M (1977) Dynamics of aggression in male pumpkinseed sunfish (*Lepomis gibbosus*) over the reproductive phase. *Z Tierpsychol* 43:139–151
- Colgan P, Nowell W, Gross M, Grant JWR (1978) Aggressive habituation and rim circling in the social organization of *Lepomis macrochirus* sunfish. *Environ Biol Fish* 4:29–36
- Courtenay W, Sahlman H, Miley W, Herrema D (1974) Exotic fishes in fresh and brackish waters of Florida. *Biol Conserv* 6:292–302
- Crossman E (1991) Introduced freshwater fishes: a review of the North American perspective with emphasis on Canada. *Can J Fish Aquat Sci* 48:46–47
- Dame E, Petren K (2006) Behavioural mechanisms of invasion and displacement in Pacific island geckos (*Hemidactylus*). *Anim Behav* 71:1165–1173
- Draud M, Lynch P (2002) Asymmetric contests for breeding sites between monogamous pairs of convict cichlids (*Archocentrus nigrofasciatum*): pair experience pays. *Behaviour* 139:861–873
- Draud M, Macias-Ordóñez R, Verga J, Itzkowitz M (2004) Female and male Texas cichlids (*Herichthys cyanoguttatus*) do not fight by the same rules. *Behav Ecol* 15:102–108
- Dubois F, Giraldeau LA, Hamilton IM, Grant JWA, Lefebvre L (2004) Distraction sneakers decrease the expected level of aggression within groups: a game-theoretic model. *Am Nat* 164:E32–E45
- Enquist M, Leimar O, Ljungberg T, Mallner Y, Segerdahl N (1990) A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. *Anim Behav* 40:1–14
- Fuentes GN, Cashner RC (2002) Rio Grande cichlid established in the Lake Pontchartrain drainage, Louisiana. *Southwest Nat* 47: 456–459
- Fuller PL, Nico LG, Williams JD (1999) Nonindigenous fishes introduced into inland waters of the United States. Special Publication 27. American Fisheries Society, Bethesda
- Glova GJ (2003) A test for interaction between brown trout (*Salmo trutta*) and inanga (*Galaxias maculatus*) in an artificial stream. *Ecol Freshw Fish* 12:247–253

- Grand TC, Grant JWA (1994) Spacial predictability of food influences its monopolization and defence by juvenile convict cichlids. *Anim Behav* 47:91–100
- Gunckel SL, Hemmingsen AR, Li JL (2002) Effect of bull trout and brook trout interactions on foraging habitat, feeding behavior, and growth. *Trans Am Fish Soc* 131:1119–1130
- Hubbs C, Lucier T, Garrett G, Edwards R, Dean S, Marsh E (1978) Survival and abundance of introduced fishes near San Antonio, Texas. *Tex J Sci* 30:369–376
- Human KG, Gordon DM (1999) Behavioral interactions of the invasive Argentine ant with native ant species. *Insectes Soc* 46:159–163
- Keeley ER, Grant JWA (1993) Visual information, resource value and sequential assessment in convict cichlids (*Cichlasoma nigrofasciatum*) contests. *Behav Ecol* 4:345–349
- Klocker CA, Strayer DL (2004) Interactions among an invasive crayfish (*Orconectes rusticus*), a native crayfish (*Orconectes limosus*), and native bivalves (Sphaeriidae and Unionidae). *Northeast Nat* 11:167–178
- Leiser JK, Gagliardi JL, Itzkowitz M (2004) Does size matter? Assessment and fighting in small and large size-matched pairs of adult male convict cichlids. *J Fish Biol* 64:1339–1350
- Lorenz OT, O'Connell MT (2008) Growth of non-native Rio Grande cichlids (*Herichthys cyanoguttatus*) at different salinities and in the presence of native bluegill (*Lepomis macrochirus*). *J Freshw Ecol* 23:537–544
- Marchetti MP (1999) An experimental study of competition between the native Sacramento perch (*Archoplites interruptus*) and introduced bluegill (*Lepomis macrochirus*). *Biol Invasions* 1:55–65
- Matsumoto K, Kohda M (2004) Territorial defense against various food competitors in a Tanganyikan benthophagous cichlid, *Neolamprologus tetracanthus*. *Ichthyol Res* 51:354–359
- Maynard Smith J (1974) Theory of games and the evolution of animal contests. *J Theor Biol* 47:209–221
- Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, London
- Metcalf NB, Valdimarsson SK, Morgan IJ (2003) The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. *J Appl Ecol* 40:535–544
- O'Connell MT, Fuentes GN, Cashner RC (2002) Application of a diffusion model to describe a recent invasion; observations and insights concerning early stages of expansion for the introduced Rio Grande cichlids in southeastern Louisiana. *Aquat Invader* 13:1–5
- Ratnasabapathi D, Burns J, Soucek R (1992) Effects of temperature and prior residence on territorial aggression in the convict cichlid, *Cichlasoma nigrofasciatum*. *Aggress Behav* 18:365–372
- Rincon PA, Correas AM, Morcillo F, Risueno P, Lobon-Cervia J (2002) Interaction between the introduced eastern mosquitofish and two autochthonous Spanish toothcarps. *J Fish Biol* 61:1560–1585
- Ross ST (2001) The inland fishes of Mississippi. University Press of Mississippi, Jackson
- Schrank SJ, Guy CS, Fairchild JF (2003) Competitive interactions between age-0 bighead carp and paddlefish. *Trans Am Fish Soc* 132:1222–1228
- Turner GF (1994) The fighting tactics of male mouthbrooding cichlids: the effects of size on residency. *Anim Behav* 47:655–662
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science* 277:494–499
- Warburton K, Madden C (2003) Behavioural responses of two native Australian fish species (*Melanotaenia duboulayi* and *Pseudomugil signifer*) to introduced poeciliids (*Gambusia holbrooki* and *Xiphophorus helleri*) in controlled conditions. *Proc Linn Soc NSW* 124:115–123
- Wazlavsek BE, Figler MH (1989) Territorial prior residence, size asymmetry, and escalation of aggression in convict cichlids (*Cichlasoma nigrofasciatum*). *Aggress Behav* 15:235–244
- Wildhaber ML, Green RF, Crowder LB (1994) Bluegills continuously update patch giving-up times based on foraging experience. *Anim Behav* 47:501–513
- Wilson EO (1975) Sociobiology: the new synthesis. Harvard University Press, Cambridge