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ORIGINAL PAPER

Nonnative African jewelfish are more fit but not bolder at the invasion front: a trait comparison across an Everglades range expansion

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Abstract Invasive species present a global threat to natural ecosystems and native biodiversity. Previous studies have shown that invasive range expansion is often related to the invader's life histories and dispersal behavior. Among behavioral traits, boldness is a key trait that may aid species in performing well in novel environments. Thus, along a species' invaded range, individuals from the invasion front should be bolder, better dispersers, and have life histories that maximize population growth relative to established populations. We tested these hypotheses with the invasion of the African jewelfish *Hemichromis letourneuxi* in Everglades National Park (ENP). Jewelfish entered ENP in 2000, and since then they have expanded their range rapidly but traceably. Our study examined variation in reproductive investment, body condition, gut fullness, boldness, and dispersal behavior across six wild-caught populations of African jewelfish. Boldness and dispersal were tested using an emergence-activity test and an emergence-dispersal test in large, outdoor experimental setups. We dissected fish from the six populations to assess life histories. Populations from the invasion front (western ENP) had higher reproductive investment, higher gut fullness, and better body condition, but they were not relatively bolder nor better dispersers than inner populations (eastern ENP). As the invasion progressed, lower intraspecific density at the invasion front may have relaxed competition and allowed for higher fitness and reproductive investment. Understanding underlying behavioral and life-history mechanisms of an invasion is key for the development of management strategies that aim to contain current invaders and prevent the spread of future ones.

Keywords Range expansion · Fish · Boldness · Dispersal tendency · Life history traits · Invasion front

Introduction

Worldwide, anthropogenic stressors are causing species distributions to change. Climate change, land-use change, habitat fragmentation/loss, and species translocations are resulting in dramatic range shifts, contractions, and expansions among native and nonnative taxa (Case and Taper 2000; Parmesan and Yohe 2003; Sato et al. 2010). These distributional changes are often accompanied by new selection pressures (Suarez and Tsutsui 2008), as organisms encounter novel habitats, environmental conditions, and biotic interactions (e.g., HIREC or human-induced rapid environmental change; Sih et al. 2011). For example, organisms moving into urban environments may experience relaxed predation and higher resource levels relative to natural habitats (Gilroy and

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Sutherland 2007). Permanence and range expansion by invaders in a new environment requires phenotypic and/or evolutionary trait responses that maximize individual fitness (Ghalambor et al. 2007; Hendry et al. 2008).

Although an extensive body of theoretical work addresses the potential mechanisms that drive range expansions, as well as limit species distributions (Burton et al. 2010; Holt et al. 2005; Hughes et al. 2007; Kubisch et al. 2010), additional empirical work is needed to understand the complexity of range dynamics in nature (Holt et al. 2005). In the initial stages of an invasion, phenotypic plasticity likely allows organisms to tolerate novel conditions and eventually adapt to the new environment (Ghalambor et al. 2007). For instance, as invaders colonize new territories, they often invest more energy into reproduction in response to lower conspecific density and competition at the leading edge of the range (Burton et al. 2010; Phillips et al. 2008; Travis and Dytham 2002). They also evolve life-history strategies such as higher growth rates to offset the high costs of novelty (Phillips 2009).

Understanding of range expansion dynamics necessitates that a species' distribution is clearly demarcated. However, knowledge of the invasion history of a non-native organism is often difficult to acquire due to unknown invasion origins and multiple introduction events (i.e., Collins et al. 2002; Kolbe et al. 2004). Further, the record of spread is equally difficult to observe and track (Lodge et al. 2006), especially in highly-mobile animals that disperse long distances (Nathan et al. 2003). For instance, among vertebrate invaders, fourteen studies focused on only three well-studied invasions are able to closely track invader spread and range expansion (Table 1). The invasion of cane toads, *Rhinella marinus*, in Australia provides one of the few instances where the invasion sequence is well-known (Phillips et al. 2007), giving us somewhat of a unique opportunity to track behavioral, morphological and life-history adaptations and/or plastic responses that accompany the range expansion (Alford et al. 2009; Llewelyn et al. 2010; Phillips et al. 2006; Phillips 2009; Urban et al. 2008). For example, invasion front cane toads showed an accelerated rate of range expansion (Urban et al. 2008), higher

Table 1 Summary of previous animal studies comparing traits between invasion front and established populations

Taxa	Traits favored at invasion front	Mechanism leading to trait differences	Reference	Evolution/ Plasticity
Rhinella marinus	Dispersal	Heritability	Phillips et al. (2010a)	Evolution
Rhinella marinus	Dispersal ability	Endurance	Llewelyn et al. (2010)	Evolution
Rhinella marinus	Growth rate	Early reproduction	Phillips (2009)	Evolution
Rhinella marinus	Dispersal	Path straightness, movement length	Alford et al. (2009)	Evolution
Rhinella marinus	Rate of invasion	Long-distance jump dispersal, abiotic conditions	Urban et al. (2008)	Evolution/ plasticity
Rhinella marinus	Dispersal behavior	Cannibalistic conspecifics	Child et al. (2008)	Unknown
Rhinella marinus	Dispersal rate	Movement distance and duration	Phillips et al. (2008)	Evolution
Rhinella marinus	Movement rate	Abiotic conditions	Phillips et al. (2007)	Evolution/ plasticity
Rhinella marinus	Long-distance movement	Road corridors	Brown et al. (2006)	Unknown
Rhinella marinus	Dispersal speed	Leg length	Phillips et al. (2006)	Evolution
Sialia mexicana	Dispersal, reproduction	Aggression	Duckworth (2008)	Evolution
Sialia mexicana	Dispersal	Aggression	Duckworth and Badyaev (2007)	Evolution
Sturnus vulgaris, *Carpodacus mexicanus*	Propagule dispersal	Habitat quality	Gammon and Maurer (2002)	Unknown
Neogobius melanostomus	Gut fullness index and condition factor	Prey composition	Raby et al. (2010)	Unknown

dispersal rates, and higher individual growth rates compared to populations behind the leading edge (Phillips 2009; Phillips et al. 2010a; Table 1). Similarly, the recolonization of western bluebirds (*Sialia mexicana*) over the northwestern United States has been facilitated by the coupling of high levels of aggression and dispersal in populations at the leading edge (Duckworth and Badyaev 2007). These studies highlight the importance of both life history and behavioral plasticity and/or evolution at the expanding edge of an invasion (Sih et al. 2011; Table 1).

Among behavioral traits, boldness, defined as the propensity of individuals to explore unfamiliar space and take risks (Wilson et al. 1993; Wilson et al. 2010), has been shown to be a key trait underlying invasion success (Cote et al. 2010; Rehage and Sih 2004). Yet, whether boldness is also an advantageous trait at the leading edge of an invasive range expansion is not known. Boldness may play a role in the dispersal of organisms since bold individuals willing to move through space and take risks are better dispersers than shy ones (Fraser et al. 2001). The coupling of boldness and dispersal tendency could be a highly-favored trait combination at the invasion front, leading to rapid spread, and possibly resulting from spatial sorting (Shine et al. 2011). In this study, we examined variation in boldness, dispersal tendency, and life histories across populations of a recent fish invader in the Florida Everglades to better understand the relative role of these traits in range expansion.

Eighteen non-native fish species are currently established in Everglades National Park (ENP; Shafland et al. 2008; J. Kline, pers. comm.). Among those, a recent invader is the African jewelfish *Hemichromis letourneuxi,* a small predatory cichlid (Dunlop-Hayden and Rehage 2011; Rehage et al. 2009), introduced to urban canals in South Florida in the 1960's (Rivas 1965). Jewelfish were first detected in ENP in 2000 along the eastern boundary of the park (Chekika area, Fig. 1), and since then have rapidly spread westerly at a rate of approximately 4 km/year. It is suspected that the invasion was an unintended consequence of restoration efforts that increased hydrological connectivity between ENP marshes and the bordering L31W canal (J. Kline, unpubl. data; Fig. 1). This invasion then provides a unique opportunity to track the range expansion and spread of a fish invader across the landscape. By comparing three invasion front and three established populations, we examined behavioral and life history traits that may favor their rapid colonization across the Everglades. Using dissected wild-caught fishes from the six populations, we compared fish condition, gut fullness, and reproductive allocation. In videotaped behavioral assays, we compared boldness, and dispersal tendency of wild caught fish from the same six populations. Dispersal tendency refers to the propensity of individuals to move across relatively long distances, and is expected to be correlated to true measures of field dispersal (Fraser et al. 2001; Kobler et al. 2009; Rehage and Sih 2004).

Following Burton et al. (2010), we hypothesized that invasion front populations of African jewelfish in ENP would allocate more resources to reproduction and be better dispersers than established populations. Because dispersal and boldness have been shown to be correlated (Duckworth and Badyaev 2007; Fraser et al. 2001; Rehage and Sih 2004), we also expected frontier populations to be bolder than established ones. Bold individuals are highly exploratory and active (Wilson and Godin 2009), which may be advantageous if individuals encounter novel conditions. As the invasion proceeds, advancing populations may experience low intraspecific competition (Phillips et al. 2010a; Travis and Dytham 2002), coupled with naïve prey (Dunlop-Hayden and Rehage 2011; Rehage et al. 2009; Sih et al. 2010). Thus, jewelfish at the frontier may experience high abundance of resources (Bohn et al. 2004), and better foraging opportunities. We expected fish from the invasion front to be in better condition, and have greater allocation to reproduction relative to populations behind the leading front.

Methods

Study system

Over the past 11 years, African jewelfish have spread from the eastern boundary of ENP to western marshes and coastal mangroves (Fig. 1). The marsh region that was first invaded and inhabited the longest by jewelfish is a karst graminoid wetland with relatively short-hydroperiod (5–6 months of flooding over the year; Kobza et al. 2004). Because of the short duration of flooding, these habitats are predator-limited (Chick et al. 2004), and community structure is dominated by small

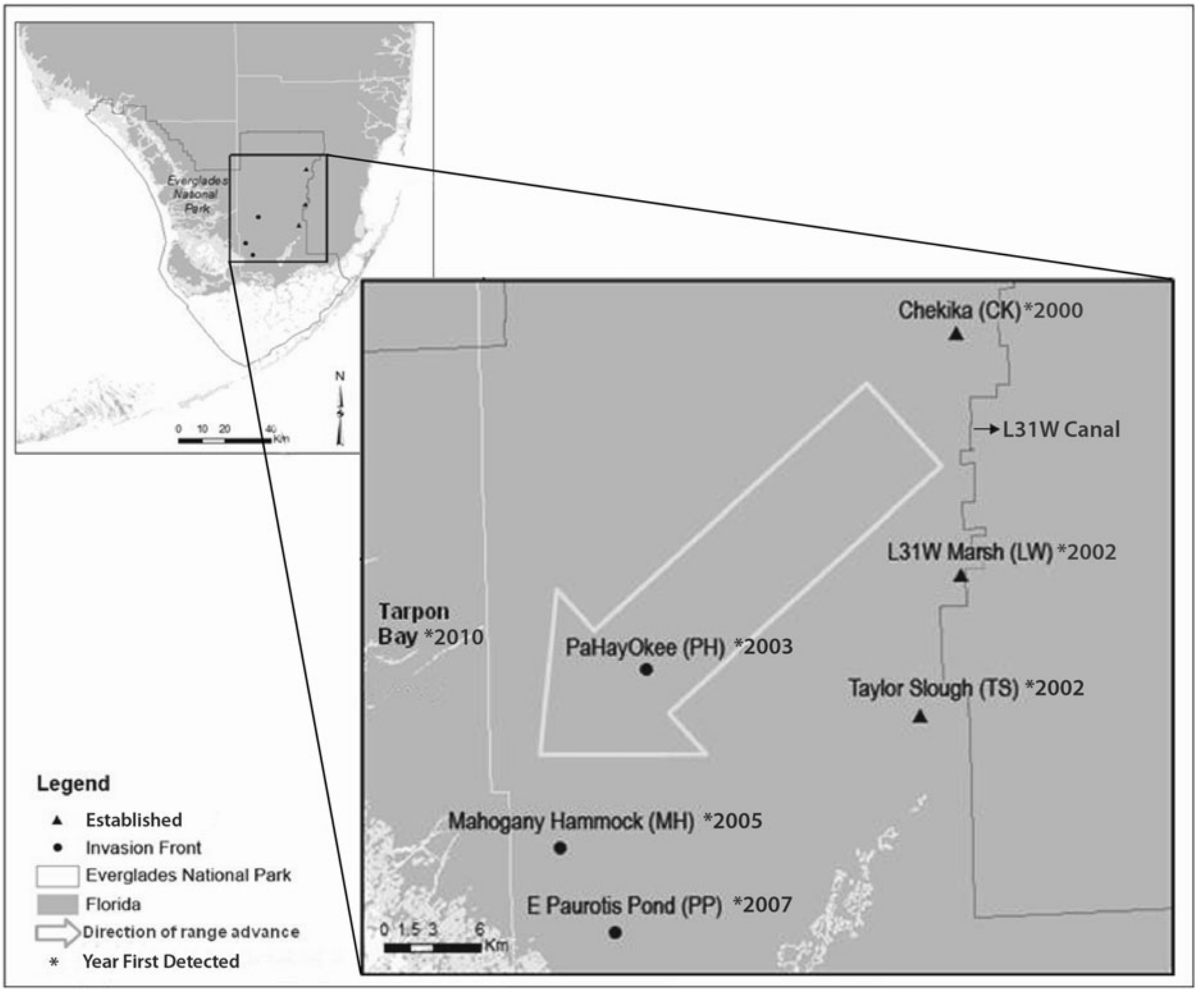

Fig. 1 Map of Everglades National Park (ENP) showing the location of African jewelfish study populations (invasion front and established) the direction of range advance, and estimated date of arrival of each population

poeciliids, centrarchids, and other nonnative cichlids (particularly Mayan cichlid, *Cichlasoma urophthalmus,* and Black acara, *Cichlasoma bimaculatum*; Kobza et al. 2004). The marsh surface is also dotted by a mosaic of depressions in exposed limestone outcroppings from a few cm to >100 cm deep. These solution holes serve as important dry season refugia for many aquatic organisms (Kobza et al. 2004; Ruetz et al. 2005). Seasonal movement by fishes in and out of these dry-down refugia (and others, e.g., alligator holes, mangrove creeks; Palmer and Mazzotti 2004; Rehage and Loftus 2007) is critical to individual survival and population persistence (Chick et al. 2004; Obaza et al. 2011). Thus, we expect dispersal to be an adaptive trait for Everglades native fishes, as well as for recently arrived non-native taxa.

We collected African jewelfish from six sites within ENP in the summer and early fall of 2009. A total of 256 jewelfish were used to assess life histories, and 192 fish for behavioral trials (Table 2). Three of the populations correspond to the invasion front on the western part of ENP (PH, MH, and PP, Fig. 1), while the other three are better established populations (hereafter referred to as established) along the eastern boundary of the park (CK, LW and TS). All fish were collected using unbaited minnow traps randomly deployed in marshes, including near road culverts and canals at 30–100 cm water depth. Trapping techniques can exhibit sampling inefficiencies and biases, including when attempting to capture mixed behavioral types (i.e., shy and bold individuals; Biro and Dingemanse 2009). Work by Wilson et al. (1993)

Table 2 Location and details of fish collections (N) for the behavioral assays (B) and life history assessment (LH)

Sampling site	Location	Distance to CK (Km)	Test	Collection dates	N_{LH}	N_B	N_{total}
Invasion front							
Pahayokee (PH)	25°26′N;	18	B	8 July–16 July 2009	46	32	78
	80°47′W		LH	21 Aug–25 Sept 2009			
Mahogany	25°20′N;	25	B	8 July–9 July 2009	34	32	66
Hammock (MH)	80°50′W		LH	19 Aug–20 Aug 2009			
East of Paurotis	25°17′N;	26	B	16 July–23 July 2009	33	32	65
Pond (PP)	80°48′W		LH	19 Aug–21 Aug 2009			
Established							
Chekika (CK)	25°37′N;	_	B	16 Aug–17 Aug 2009	37	32	69
	80°35′W		LH	3 Oct 2009			
L31W Marsh (LW)	25°28′N;	10	B	8 July–14 Aug 2009	40	32	72
	80°35 W		LH	8 Oct 2009			
Taylor Slough (TS)	25°24′N;	15	B	23 July–13 Aug 2009	66	32	98
	80°36′W		LH	28 Aug–25 Sept 2009			
				Total	256	192	448

showed that minnow traps were more likely to capture bold pumpkinseed sunfish instead of shy ones. We expect that these biases likely result from various sampling techniques, but if populations truly differ, we should be able to detect behavioral type differences despite these potential biases in collecting methodology.

Life history traits

Fish captured for life history assessments were euthanized immediately at capture with an overdose of the anesthetic MS-222 (Nickum et al. 2004), fixed in 10 % formalin, and preserved in 70 % ethanol. In the laboratory, all fish were measured in mm standard length (SL), weighed to the nearest 0.01 g, and dissected to determine gender, allocation to reproduction, and gut contents. We calculated fish condition (K), as the ratio of the fish's body weight (W) and SL (Williams 2000):

$$K = 100000\,W(g)/SL^3(mm)$$

During dissections, all stomach contents were extracted (including detritus) and weighed individually to calculate a gut fullness index (GFI; Yanagisawa and Sato 1990). Small fishes and grass shrimp were easily identified in the majority of stomach contents (Jungman et al., unpubl. data).

$$(GFI) = \text{wet weight of gut contents}\,(g)/\\ \text{wet body weight}\,(g) \times 100$$

We then used a gonadosomatic index (GSI) to quantify the reproductive investment of females (Bohn et al. 2004; Kreiner et al. 2001):

$$(GSI) = \text{wet weight of gonad}\,(g)/(\text{wet body weight}\,(g)\\ - \text{Gonad wet weight}\,(g)) \times 100$$

Separate generalized linear mixed models (GLMM; Proc Mixed in SAS 9.2) were fitted to the life histories using K, GFI, or GSI as dependent variables, and population type (invasion front vs. established) as the main fixed effect. Population nested within population type was fitted as the random effect (Bolker et al. 2009). For the K and GFI models, gender was added as an additional fixed effect. Significance for the random effect was determined by using a log-likelihood ratio test, which follows a Chi-square distribution (i.e., Newman-Pearson criterion; Kurvers et al. 2009). Because the GFI and GSI residuals were not normal, they were log-transformed prior to analyses (Bland and Altman 1996).

Behavioral assays

Fish used in behavioral assays were captured from the same six focal populations (Table 2), brought back to the laboratory, and housed in outdoor 795 l tanks separated by population until trial dates (2–4 months). Some populations required considerable effort to collect, possibly because collections were made in the wet season, when fish were dispersed over the landscape or due to lower densities (although these were not quantified). This holding period falls within the range of other published behavioral studies, including ones assessing boldness and dispersal behavior (1–6 months; Cote et al. 2010, 2011; Harcourt et al. 2010; Ioannou et al. 2008; Schurch and Heg 2010). Stock populations were maintained at similar densities and were fed a combination of live prey (dominated by native mosquitofish, *Gambusia holbrooki*), frozen bloodworms, and fish food flakes ad libitum.

We quantified boldness and dispersal tendency of the six populations in outdoor experimental tanks (Fig. 2). Trials were conducted between November 12 and December 7, 2009. Because jewelfish are highly social (Loiselle 2000; Rehage et al. 2009; Schofield et al. 2007), we used pairs of individuals for all behavioral trials. Previous assays of dispersal have also used groups instead of solitary individuals (Cote and Clobert 2010; Gilliam and Fraser 2001; Meylan et al. 2009; Rehage and Sih 2004). Dispersing fishes may rely on social information to navigate their environments (Frost et al. 2007), and to facilitate decision making (Seppanen et al. 2007). A total of 16 pairs per population were videotaped over 4 blocks (6 populations per day × 4 days per block × 4 blocks = 96 fish pairs), with a replicate of each population tested daily, in two consecutive behavioral assays. For all pairs, a boldness assay (hereafter Boldness1) was conducted between 09:00 and 12:00, followed by a combined boldness and dispersal tendency assay conducted between 13:00 and 17:00 (hereafter Boldness2-Dispersal). For all pairs, we allowed at least 4 h between the two assays, such that the order of fish pairs tested in the morning trials was the same as the afternoon tests. Since temperature may have a strong influence on behavioral parameters (Biro et al. 2010), water temperature was recorded at the beginning of each trial. At the end of the experiments, fish were euthanized with an overdose of MS-222, measured, weighed, fixed in 10 % formalin for 2–5 days, and stored in 70 % ethanol for later gender determination via dissection.

Boldness1 assay

We characterized boldness using a standard emergence test; shown to be an effective method to measure boldness and exploratory behavior (Bell 2005; Brown et al. 2005; Wilson and Godin 2009). In an emergence test, fish were added to a novel arena, placed in a refuge, and the time to emerge from the refuge was quantified, with the notion that bolder individuals would emerge sooner. The experimental tank included a refuge box (21 × 30 × 30 cm) placed at the bottom and center of a 795 l outdoor tank (Fig. 2a). The box was equipped with a removable door that allowed fish

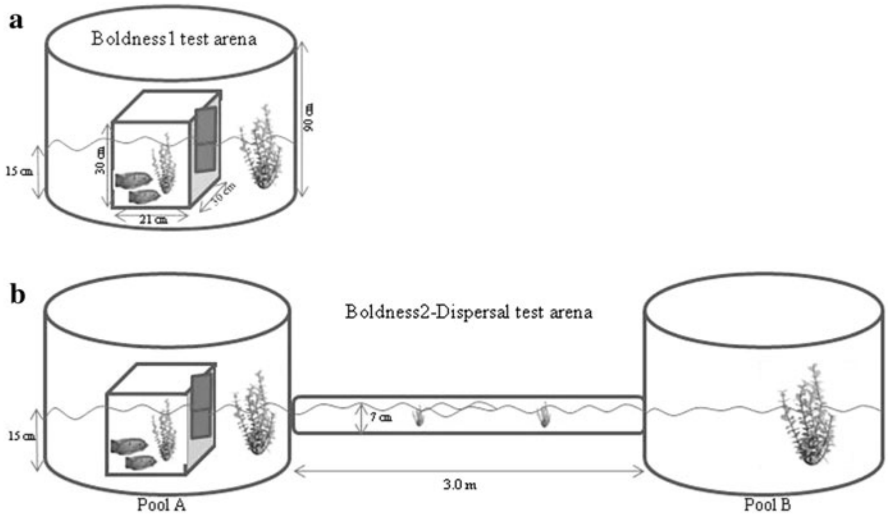

Fig. 2 Diagram of experimental set up for assessing (**a**) Boldness1, and **b** Boldness2-Dispersal across African jewelfish fish pairs from the six study populations

to emerge. Artificial plants were placed inside and outside the refuge box to provide structure, and gravel was used as substrate. The water depth was kept at 15 cm to prevent subjects from swimming above the refuge and the artificial plant, thus information about the environment could only be gained by moving around these objects. We recorded fish behavior using a Sony DCR-SX41 digital video camera mounted directly above the boldness setup to give a full top view of the experimental tank.

For each trial, we selected a random pair of fish from a stock tank, placed them into the refuge box (Fig. 2a), and gave them a 10-min acclimation period. At the end of this period, the trapdoor was remotely and gently lifted (using a 150 cm line pulled from behind a blind), and the fish pair was free to emerge and explore the tank arena for 20 min. The following timed parameters (in seconds) were recorded: (1) latency to emerge, (2) proportion of trial time spent back in the refuge (added for all returns to the refuge post the first emergence), (3) proportion of time spent in the artificial plant outside of the refuge, and (4) proportion of time spent swimming in open water. Fish that did not emerge from the refuge were assigned a maximum latency to emerge score of 1,200 s, and no further behavioral measures were conducted on these individuals. At the end of each Boldness1 trial, the pair was removed from the tank, placed in a separate holding tank (35 × 20 × 13 cm) until the Boldness2-Dispersal test was conducted in the afternoon.

Boldness2-Dispersal assay

For the second behavioral assay, the setup was similar to the Boldness1 setup with an identical emergence tank (center refuge box, gravel, and artificial vegetation inside and outside the refuge in the same locations), plus a 3 m long channel (35 cm wide), which connected the emergence tank to a second tank, where the fish could disperse and explore a new area (Fig. 2b). In this setup, both tanks and the channel were covered with gravel as a substrate, and in the second tank, habitat complexity was similar to that of the emergence tank (one artificial plant placed near the center). In this assay, we characterized the repeatability of boldness, as well as the dispersal tendency of the subjects by giving them the opportunity to explore and move into a new area of the experimental setup (Fig. 2b). Movement from the emergence tank to the second tank through the connecting channel (Fig. 2b) mimics the movement of Everglades fishes in and out of dry-down refugia as water level fluctuate seasonally (Kobza et al. 2004).

Similarly to Boldness1, fish pairs were removed from the holding tank, placed in the refuge box (Fig. 2b), and given a 10-min acclimation period. Following acclimation, the trapdoor was opened, and behaviors were recorded for 20 min. For this assay, a second video camera recorded the full view of the channel, which was marked every 30 cm with bright colored tape to allow the observer to note the distance covered by dispersing fish. From the two recordings, we extracted measures of the same four behaviors recorded in Boldness1, with the exception that time spent swimming here also included time spent swimming in the new area (i.e., original pool, plus channel and second pool). In addition, we measured another four behaviors: (5) latency to disperse (the time fish first entered the channel), (6) the number of dispersal attempts (the number of times fish entered the channel), (7) maximum dispersal distance across all dispersal attempts (in m, if fish reached the second tank, the maximum distance of 3 m was given), and (8) the proportion of trial time spent in the new environment [(time spent in channel + second pool)/20 min trial time]. As in Boldness1, fish that did not exit the refuge were assigned a maximum latency to emerge score of 1,200 s. Similarly, those fish that emerged but did not disperse were assigned a maximum latency to disperse score of 1,200 s. All fish pairs were tested in both trials (Boldness1 and Boldness2-Dispersal), and all data were included in statistical analyses. All behavioral variables were quantified by a single observer (D.P.L.) using JWatcher® (v1.0; http://www.jwatcher.ucla.edu/).

From the videotapes, we quantified behavioral data separately for each focal fish, and averaged the scores to obtain a pair mean to be used in all analyses. The four variables recorded in Boldness1 were incorporated into a principal component analysis (PCA; Bell and Stamps 2004). The first principal component score (hereafter B1) from the Boldness1 assay explained 75.4 % of the variance (Table 3). Similarly, the eight behavioral variables measured in the Boldness2-Dispersal test were tested in a second PCA. The first two principal component scores in this analysis explained 87.7 % of the variance. The second principal component score loaded in the same direction as in B1 (Table 3) and was

Table 3 Results of principal component analyses on behavioral measures

Behavioral traits Boldness1	PCA Loadings B1		Cumulative (%) variation explained
Latency to emerge	**0.5299**		75.4
Proportion of time back in refuge	**0.5608**		
Proportion of time in outside plant	**−0.4345**		
Proportion of time swimming	**−0.4647**		
Boldness2-Dispersal	B2	D1	Cumulative (%) variation explained
Latency to disperse	−0.1736	**−0.4022**	64.8
Maximum dispersal distance	0.1935	**0.4070**	
Number of attempts to disperse	0.1961	**0.3913**	
Proportion of time in new area	0.2306	**0.3745**	
Proportion of time swimming	−0.0114	**0.4084**	
Latency to emerge	**0.3792**	−0.3327	87.7
Proportion of time back in refuge	**0.4806**	−0.3161	
Proportion of time in outside plant	**−0.6825**	0.0245	

Loadings and explained variance are given for the emerging axes. Bold font indicates the boldness and dispersal dimensions defined by PCA factor loadings

designated as B2. Dispersal dimensions were explained by the first principal component score designated D1 (Table 3). Boldness and dispersal dimensions were defined with PCA factor loadings greater than 0.32 (Tabachnick and Fidell 1996). B1, B2, and D1 PCA scores were used in further analyses (Table 4). Since low PCA scores corresponded to bold pairs, we inverted the scale by reversing the sign of B1 and B2 scores to aid in interpretation of results (Bell 2005; Dingemanse et al. 2007).

We fitted a generalized linear mixed model (GLMM; Proc Mixed in SAS 9.2) to B1 and B2 scores together (Table 4). Main fixed effects included population type (invasion front vs. established), trial (B1 vs. B2), water temperature, condition factor (averaged for the pair), and gender of the pair (female, male, or mixed, determined from post-trial dissections). Population nested within population type was fitted as a random effect (Bolker et al. 2009). A separate GLMM using the same fixed and random effects (except for trial) was fitted to D1 scores. Significance for the random effect was determined as described in the life history analysis. We tested the relationship between Boldness1 and Dispersal with a simple linear regression (Brown et al. 2005).

Results

Life history trait variation

We found differences in life history traits between invasion front and established populations of non-

Table 4 GLMM results examining the effects of population type (invasion front vs. established), trial (B1 vs. B2), body condition, water temperature, and gender (M, F, or mixed) on boldness and dispersal measures

Effects	Boldness1 and Boldness2			Dispersal		
	df	*F*	*P*	*df*	*F*	*P*
Fixed						
Population type	1, 6	0.2	0.64	1, 6	1.2	0.32
Trial	1, 185	0.01	0.91	–	–	–
Condition factor	1, 165	1.1	0.30	1, 96	1.9	0.18
Water temperature	1, 187	0.5	0.49	1, 90	0.6	0.44
Gender	2, 190	0.6	0.56	2, 93	0.0	1.00
Random						
Population (population type)	–	–	>0.05	–	–	<0.01

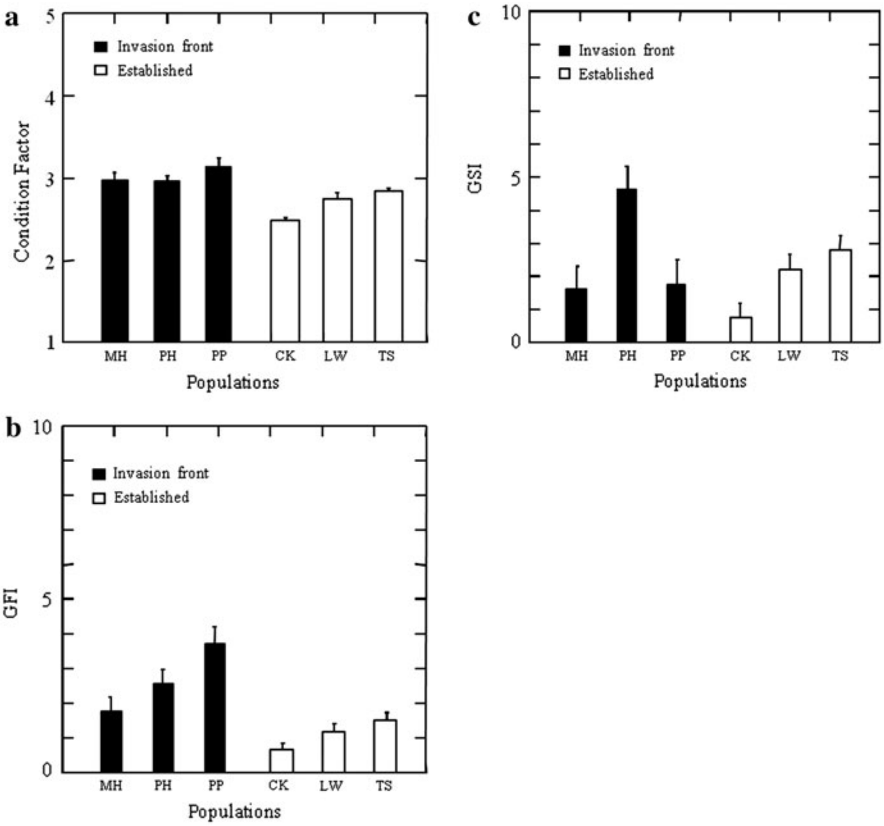

Fig. 3 Life history trait variation in African jewelfish between invasion front and established populations in **a** body condition (K), **b** gut fullness index (GFI), and **c** gonadosomatic index (GSI)

native African jewelfish from ENP. Condition factor and gut fullness index from frontier populations were significantly and consistently higher than those of the established populations (Fig. 3; Table 5). Females across population types were in better condition than males. Likewise, reproductive traits displayed significant spatial variation, but here the effect was less consistent. On average, females from the invasion front showed higher reproductive investment than females from established populations, but this trend was driven by the disparity between only two of the six populations (PH vs. CK; Fig. 3c; Table 5). Population-level variation was detected across all life history measures (Fig. 3; Table 5).

Table 5 GLMM results examining the effects of population type (invasion front vs. established), population (CK, LW, TS, PH, MH, and PP), and gender on the life history traits of jewelfish

Effects	Condition factor (K)			Gut fullness index (GFI)			Gonadosomatic index (GSI)		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Fixed									
Population type	1, 4	8.0	**0.05**	1, 252	24.2	**<0.0001**	1, 116	3.6	**0.05**
Gender	1, 251	15.7	**<0.0001**	1, 252	0.2	0.64	–	–	–
Population type × gender	1, 251	0.5	0.48	1, 252	0.7	0.41	–	–	–
Random									
Population (population type)	–	–	**<0.01**	–	–	**<0.01**	–	–	**<0.01**

Significant effects are bolded

Behavioral traits

Boldness1

Movement and exploratory behaviors (i.e., proportion of time swimming and proportion of time using habitat structure) loaded negatively and opposite to shy behaviors (i.e., proportion of time back in the refuge and latency to emerge, Table 3). From the PCA results, we considered pairs with a B1 above 1 to be bold, pairs with scores between 0 and 1 intermediate, and those with scores less than 0 as shy. Bold subjects had low emergence times, spent more time exploring the tank, and spent less time going back to the refuge than shy individuals. In this first assessment of boldness, roughly 40 % of the pairs from the invasion front, and 50 % from established populations emerged from the refuge. For the fish that emerged, emergence, on average, occurred at 9.5 min into the 20-min trial. Boldness1 did not differ between invasion front and established populations, and there were no significant differences among individual populations (Fig. 4).

Boldness2 and Dispersal

Influential factor loadings on component score one (D1) corresponded to dispersal variables (Table 3); including proportion of time swimming, suggesting that this particular behavior considerably affects the dispersal tendency of individuals. Since latency to disperse loaded negatively and opposite to all other dispersal variables, high D1 scores correspond to high dispersal tendency. From observations, most dispersing individuals explored the whole experimental setup accompanied by their partner, and reached the second tank after several exploratory attempts. Average emergence time for all pairs was 6 min, while for those that dispersed; dispersal took an average of 10 min and typically after 2 attempts. Overall, 70 % of jewelfish from the invasion front, and 70 % from established populations emerged from the refuge, and for those that emerged, about 17 % from the invasion front, and 32 % from established populations dispersed into the new areas of the experimental setup (Fig. 2b). We found no significant differences in dispersal tendency between invasion front and established populations (Fig. 5; Table 4). Instead, we noted a relatively high dispersal tendency for one of the established populations (L31W population; Fig. 5). Other fixed effects tested in the models (water temperature, gender, condition factor) had no effect on the behavior of jewelfish pairs (Table 4). Invasion front populations were also not bolder than established populations in the second trial (B2), and there were no significant differences among the six individual

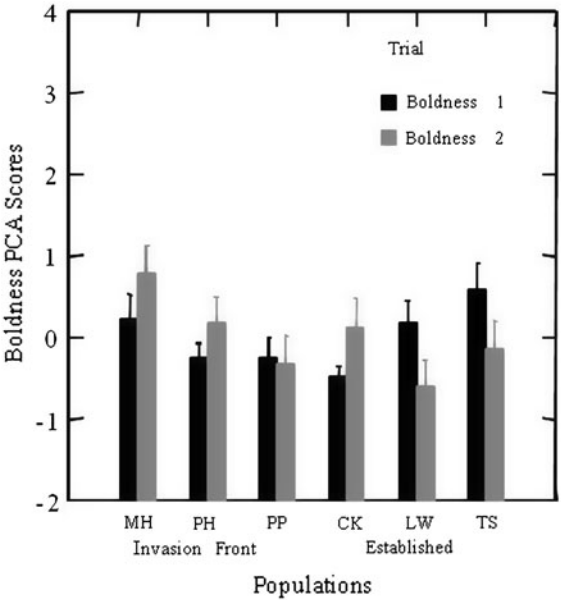

Fig. 4 PCA scores for the two boldness tests (B1 and B2) for invasion front and established populations of African jewelfish

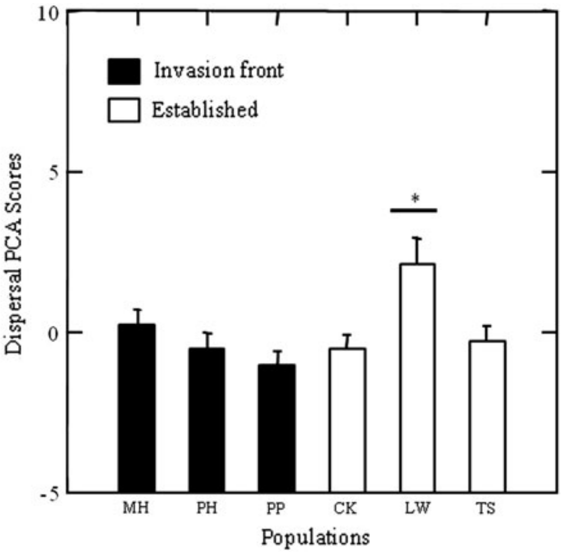

Fig. 5 PCA scores for dispersal test (D1) for the invasion front and established populations of African jewelfish

populations in these boldness scores (Fig. 4; Table 4). Correlations between B1 and D1 were very weak (Invasion front: $r^2 = 0.08$, $P = 0.05$; established: $r^2 = 0.05$, $P = 0.13$).

Discussion

Understanding the ecological and evolutionary processes that allow populations to respond to novel conditions remains an important question in the study of species distributions (Gaston 2009). Biological invasions provide an opportunity to examine the underlying mechanisms allowing rapid distributional shifts, and the limits to range expansions (Sexton et al. 2009). However, since tracking invasive spread is often difficult, few studies have examined trait variation (e.g., morphological, behavioral, and life-history) along range expansions of vertebrate invaders (Table 1). As a species colonizes a new range, population dynamics, fitness, and behaviors may shift in response to novel conditions and selection pressures (Fig. 6). A recent model by Fogarty et al. (2011) showed that certain life-history strategies coupled with a mix of behavioral types lead to higher speeds of invasion. Asocial individuals spread more quickly than their social congeners, and showed higher individual growth rates at low intraspecific density; yet a faster rate of spread was seen when a mix of behavioral types (i.e., asocial and social) was present. In this study, we examined life history and behavioral mechanisms that may help non-native jewelfish to spread in their South Florida invaded range. Jewelfish from frontier populations had higher indices of reproductive investment, condition, and gut fullness than their conspecifics from established populations. On the other hand, the coupling of boldness and dispersal tendency did not appear to be important traits facilitating spread, since fish from frontier and established populations were equally bold and showed similar dispersal behaviors in our two lab assays.

Life history trait variation

Variation in life history strategies results in response to environmental heterogeneity. In an invasion, novel conditions in both the establishment and spread phase can result in significant variation in these traits (Allendorf and Lundquist 2003; Sakai et al. 2001; Suarez and Tsutsui 2008). Comparisons of life history

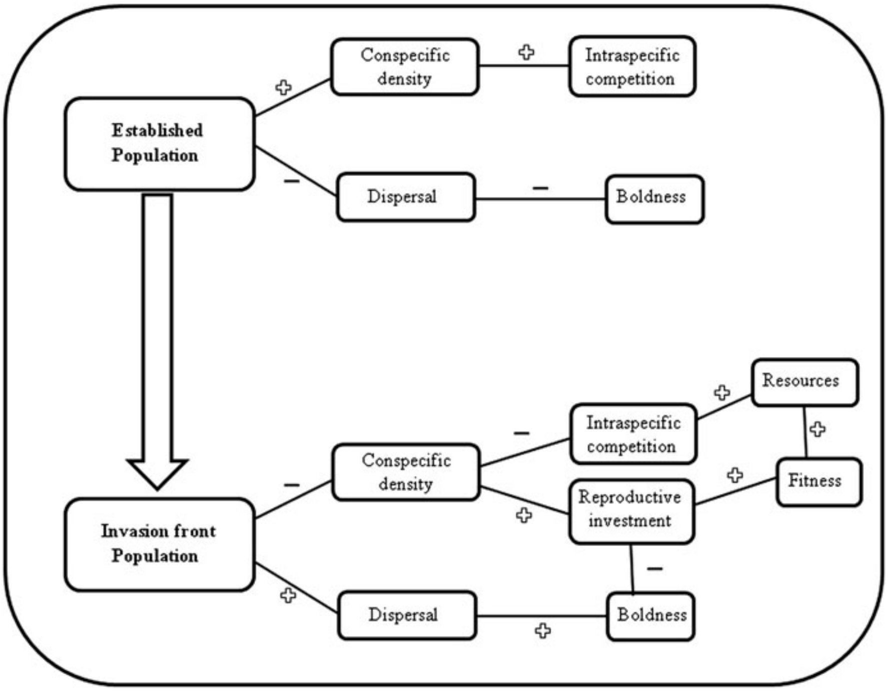

Fig. 6 Conceptual diagram of the factors driving trait variation between invasion front and established population, indicating both (+) positive and (−) negative effects

traits between a species' native and non-native range (Gurevitch et al. 2011), as well as between populations along the invaded range have provided evidence that both phenotypic plasticity and rapid evolution are driving trait variation as invaders spread (Fox et al. 2007; Joanna et al. 2011; Olden et al. 2006; Phillips 2009; Table 1). For example, the invasion of two goby species (*Neogobius kessleri* and *Neogobius melanostomus*) in the Danube river may be partially attributed to enhanced somatic condition and growth rates, resulting from improved food availability and selective predation of highly-abundant amphipods in the non-native range (Polacik et al. 2009). In invasive cane toads, rapid evolution of higher individual growth rates in the frontier populations has contributed to their accelerated range expansion in Australia (Phillips 2009). In our system, we suspect plasticity and not evolution is driving trait variation along the jewelfish range, given the rapid spread of the species and the small number of generations since jewelfish first entered ENP in 2000.

Ecological theory suggests that populations undergoing range expansion should differentially invest in dispersal and exhibit life history traits that allow for rapid colonization (Burton et al. 2010; Hughes et al. 2007; Kubisch et al. 2010; Phillips et al. 2008, 2010a; Travis and Dytham 2002). Thus, pioneer populations are expected to invest more energy in reproduction relative to established populations (Burton et al. 2010; Phillips et al. 2010b). Our life history results matched these predictions. Non-native African jewelfish from frontier populations were in better condition, invested more resources into reproduction, and had higher gut fullness than those from established populations. Possibly, higher gut fullness and body condition are a consequence of lower conspecific density, leading to higher availability of food resources or more feeding opportunities. Copeland et al. (2010) noted that changes in body condition occur as a result of factors that influence consumption. A study of round gobies (*Neogobius melanostomus*) along their invasive range in the Trent River, Ontario showed higher GFI and K in invasion front populations, due to variation in diet composition and higher resource availability between core and expanding populations (Raby et al. 2010). Higher prey abundance and more feeding opportunities may also result from prey naiveté at the expanding margin (Dunlop-Hayden and Rehage 2011; Rehage et al. 2009; Sih et al. 2010). Whether the differences in body condition and gut fullness of the focal populations here are a consequence of more feeding opportunities or differences in resource availability remains unclear. Additional sampling is needed to determine if prey availability or quality is, in fact, higher at the front of this invasion.

A reduced population density on the expanding edge of a population often drives an increase in reproductive investment (Bohn et al. 2004; Burton et al. 2010; Phillips et al. 2008, 2010a, b). Bohn et al. (2004) attributed the rapid spread of the invasive fish *Coregonus albula* along the Pasvik River to the ability of the species to be phenotypically plastic. Pioneer populations of *C. albula* traded off growth to higher reproductive investment at low densities compared to older populations at upstream sites. African jewelfish may be exhibiting plastic life history strategies, in response to lower conspecific density. It is also plausible that the lower reproductive investment of established populations is the result of their proximity to canal habitats. Predator and non-native fish abundance is higher in marshes near canals (Rehage and Trexler 2006), thus foraging success and habitat quality may be lower for jewelfish as a result of higher predation risk and/or interspecific competition (Nilsson et al. 2010).

Behavioral trait variation

Beyond life histories, behavioral mechanisms are thought to be an essential underlying component of invasion success (Brooks and Jordan 2010; Holway and Suarez 1999; Sih et al. 2011; Tuomainen and Candolin 2011). Among behavioral traits, dispersal may be the most common trait favored in populations along an invasion front, and the mechanisms leading to better dispersal are the focus of several invasive trait studies (Table 1). For example, Child et al. (2008) documented that the presence of potential cannibalistic conspecifics induces higher dispersal behavior in invasive cane toads in Australia. In western bluebirds, populations along the range edge show higher dispersal, which is positively related to aggressive behavior (Duckworth and Badyaev 2007). McCauley et al. (2010) showed that larval dragonfly that dispersed longer distances also have higher foraging efficiency. In invasive mosquitofish (*Gambusia affinis*) and native Trinidad killifish (*Rivulus hartii*), boldness has been linked to higher dispersal (Cote et al. 2010, 2011; Fraser et al. 2001; Rehage and Sih 2004). However, our results did not agree with these previous studies. We did not find a strong boldness-dispersal behavioral correlation along the invasion that could account for the rapid expansion of jewelfish in ENP. Cote et al. (2010) found that dispersal tendency was not tightly associated to a boldness-exploration-activity behavioral axis, but dispersal was more closely related to the sociability of the individuals. In their study, asocial mosquitofish (*Gambusia affinis)* tended to disperse longer distances if they originated from high-density pools.

Thus, it is possible that other sets of behaviors (i.e., aggression, voracity, or social interactions) might be more important in aiding a species to spread than dispersal tendency and boldness. Perhaps, high intra-specific density encourages moving out of a social group, since elevated conspecific aggression leads to mortality in large groups of jewelfish (Schofield et al. 2007). Alternatively, it is possible that the link between boldness and dispersal tendency may be restricted to a specific age class or gender, which was not unaccounted for in this study. Three-spined sticklebacks (*Gasterosteus aculeatus*) from a low predation site were shown to be bold and aggressive as juveniles, but these behavioral traits and the correlation between them disappeared at sub-adulthood and adulthood (Bell and Stamps 2004). Nevertheless, strong behavioral correlations remain constant throughout ontogeny in stickleback populations where predation pressure is high (Bell and Stamps 2004). Similarly, dispersal of the cichlid *Neolamprologus pulcher* in its native range is restricted to a single age class or gender (Stiver et al. 2007; Schurch and Heg 2010).

On the other hand, it may not be advantageous to behave boldly when reproductive investment is high. A model by Wolf et al. (2007) showed that traits such as boldness arise depending on the probability of future reproduction. If an individual invests highly on reproduction to obtain high fitness returns in the future, then it should be risk-averse. In contrast, risk-prone individuals invest fewer resources into reproduction. Thus, in the context of colonization, it may not be advantageous to be risk-prone (bold). Among non-native eastern mosquitofish (*Gambusia holbrooki*) introduced to Australia, female fecundity was negatively correlated to boldness. Females that put more resources into reproduction minimized predation risk, were more cautious, and took longer time to emerge from refuge (Wilson et al. 2010).

Study implications

Rapid adaptation and phenotypic plasticity in response to novel conditions (e.g., range expansion) is often driven by changes in behavioral responses (Sih et al. 2011), as well as life history variation (Bohn et al. 2004; Joanna et al. 2011; Ribeiro and Collares-Pereira 2010). By investigating the behavioral and life history mechanisms used by non-native populations to cope with novelty in their invaded range, we can better understand the role of species traits in invasions (Gurevitch et al. 2011). In addition, a framework of the key invasion processes and mechanisms for the many non-native fish currently established in ENP can provide insight for incorporating non-native fish invasion management into Everglades restoration efforts; currently a missing piece. Efforts to restore hydrological connectivity and sheetflow and to revise water delivery to the system (Rutchey et al. 2008) may provide opportunities for the containment of current invasions, and the prevention of future ones. Aside from prevention, active management strategies can be developed (e.g., management by directed evolution, MDE). MDE involves manipulating traits in order to create coexistence of native and non-native species (Davis 2009). Invasiveness could be manipulated by understanding which traits allow an invader to colonize novel territories rapidly. We expect that behavioral and life history traits are important mediators of how invasive organisms cope with and respond to environmental heterogeneity and novelty in a range expansion, and thus deserve greater attention.

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