



Anti-predatory behaviour of wild-caught vs captive-bred freshwater angelfish, *Pterophyllum scalare*

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Summary

Environments and experiences encountered in early life stages of animals shape their adult behaviour. When environments are maintained for several generations, differential selection forces act upon individuals to select those most fit to the particular conditions. As such, differences in the behaviour of captive bred and wild caught individuals have been observed recurrently. In fish, hatchery raised individuals tend to seek refuge less, making them more vulnerable to predators. We tested the hypothesis that captive breeding induces non-adaptive changes in behaviour of freshwater angelfish, *Pterophyllum scalare*. Wild-caught and captive-bred fish were exposed to a natural predator and measured for their anti-predator behaviours; no differences were found in behaviour under control conditions. When exposed to a natural predator, wild-caught fish exhibited significantly shorter freezing durations than captive-bred fish, and took significantly shorter time to resume normal behaviour. No differences in the time taken to initiate investigations of the predator were detected. The results demonstrate that captive-bred fish respond differently than their wild counterparts when exposed to a natural predator, and that this domestication has implications for captive rearing programmes.

Introduction

Rearing environments and early experiences shape an animal's behaviour (Huntingford, 2004). Animals raised in captivity encounter experiences different from their counterparts in nature. This is due to differences in resource availability, rearing densities, and dangers involved (Boersma et al., 2008; Epp and Gabor, 2008; Brockmark et al., 2010). In captivity, animals are protected from natural threats including disease, competition, and predation. Adaptations specific to the rearing environment occur when such differences prevail for several generations.

Captive rearing domesticates wild animals (Price, 1984). It habituates wild stocks to captive environments involving humans, small spaces, constant availability of food and water, and no predators (Price, 1999). Extending such a lifestyle to several generations allows to select for individuals genetically predisposed to suit these conditions (Price, 1999), such as more aggressive individuals that can compete for food, or individuals with poor predation-avoidance abilities (Huntingford, 2004). Captive conditions, as well as the lack of life training experiences present in the wild, often produce individuals unfit for wild environments (McPhee, 2003; Mathews et al., 2005; Jule et al., 2008).

Research comparing the behaviour of wild and captive animals is of particular importance to a number of applications, such as captive breeding programmes to restore wild populations. Differences have been observed in predator recognition (De Azevedo and Young, 2006), foraging (Orlov et al., 2006), and reproduction (Kelley et al., 2006) of wild and captive animals. In fish, captive breeding increases boldness (Kelley et al., 2005). Boldness is promoted by high density rearing environments, as the animals need to compete for resources (Huntingford, 2004). Some benefits of boldness in fish include increased flexibility, better ability to cope with changing environments, and more prompt resumption of normal activity (Brown and Braithwaite, 2004). Animals that resume normal behaviour sooner enjoy longer foraging durations and shorter stress durations (Braithwaite and Salvanes, 2005). Boldness, however, also includes more rapid and more frequent inspections of predators (Brown and Dreier, 2002; Kelley et al., 2005), as well as more rapid emergence from refuge. Such curiosity and increased conspicuousness makes captive-bred fish more prone to predation in the wild (Kelley et al., 2005).

Freshwater angelfish, *Pterophyllum scalare*, are cichlids native to the Amazon basin, but are now widely distributed in South America (Shukla, 2010) and have been reported in North America (Nico, 2010a). They occupy habitats with little or no water movement (Shukla, 2010), feed on invertebrates (Degani, 1993), and are preyed upon by larger piscivorous fish (Praetorius, 1932 cited in Gómez-Laplaza, 2002). *Pterophyllum scalare* are one of the few fish species found in pet stores that originate from genuinely wild and captive stocks. This species has often been used for behavioural experiments and their behavioural repertoire is therefore well documented (Gómez-Laplaza and Morgan, 1986; Saxby et al., 2010). When presented with a stimulus, angelfish exhibit a period of immobility followed by an investigatory movement towards the stimulus (Gómez-Laplaza and Morgan, 2000). As natural predators are not documented for this species, most experiments used non-native predatory fish or moving objects as stimuli (Gómez-Laplaza, 2002).

Investigating the influence of captivity on animal fitness provides valuable insight for conservation biology and for behavioural ecology. The general goal of the present study was to compare the anti-predator behaviour, specifically the ability to recognize and avoid predator cues, of wild-caught and captive-bred freshwater angelfish. We tested the hypothesis that captive breeding induces non-adaptive changes in anti-predatory behaviour. Fish were exposed to two treatments and their responses measured to visual predatory cues. Because pausing (immobility/freezing) is identified as a reliable

anti-predator response to visual cues (Pettersson and Järvi, 2006; Mesquita and Young, 2007; Malavasi et al., 2008), we assessed the presence of this response and its duration as a measure of anti-predatory behaviour.

Materials and methods

Animal strains

We acquired 12 captive-bred black marble (henceforth referred to as captive) and 14 wild-caught silver (henceforth referred to as wild) *P. scalare* of similar sizes (5–7 cm) from a local supplier. The wild fish were caught from the Nanay River by a local business in Iquitos, Peru and exported. The Peruvian supplier as well as phenotypic observations confirmed the wild origin of these individuals. Wild populations of *P. scalare* have silver bodies with dark vertical bands (Gómez-Laplaza, 2009), which was the phenotype of the wild individuals used in our experiment. Moreover, wild individuals prefer feeding in the water column whereas hatchery-reared individuals prefer surface feeding (Reinhardt et al., 2001). Throughout the experiment, wild individuals did not come to the surface to feed, but fed on settling flakes whereas captive fish always came up to the surface to feed (REB pers. obs).

A jack dempsey cichlid, *Cichlasoma octofasciatum*, served as a potential predator in our experiments. This larger and more aggressive cichlid has a native range spreading from Central America to the Amazon River basin (Burton and Burton, 2002) and has been introduced in North America (Nico, 2010b). It occupies habitats similar to those of *P. scalare* (Burton and Burton, 2002) and has been used in other behavioural experiments with non-native prey (Brown et al., 1999). The larger size and aggressive behaviour of the jack dempsey towards smaller fish make it a good predatory stimulus for this experiment (Brown et al., 1999; Brown and Dreier, 2002; Kelley et al., 2005).

Animal maintenance

Fish were kept in two circular opaque plastic containers (diameter: 66 cm, water depth: 31 cm), one for captive and one for wild fish, in a quiet room under a 12L:12D photoperiod. Opaqueness of the containers minimized any external disturbances. Fish were given at least 20 days to acclimate to their new environment. Water temperature was maintained at $25 \pm 1^\circ\text{C}$ with aquarium heaters. Water quality was maintained (0 ppm nitrate, 0 ppm ammonia) with submersible carbon filters. When nitrate or ammonia was detected, a 50–75% water change was performed. Water changes were not performed the same day fish were undergoing a trial. Fish were fed flaked tropical fish food (Nutrafin Max Complete Flake Food) once a day, with feeding always occurring after trials.

Between trials, experimental fish were kept in a rectangular glass aquarium partitioned using perforated stainless steel sheets into several rectangular cubicles (length: 7 cm \times width: 4 cm \times water depth: 24 cm). These cubicles allowed identification of the fish without using stressful tagging methods, and kept a visual and olfactory connection between the angelfish while they waited their turn. This connection is important as isolation of angelfish affects their behavioural responses (Gómez and Morgan, 1986). The external sides of the aquarium were covered with paper to reduce external interference.

The jack dempsey (henceforth referred to as JD) was acquired from the same local supplier and kept in a separate rectangular tank (60 \times 31 \times 34 cm) under the same conditions, but was provided pellet food instead of tropical flakes.

Experimental procedure

Two experimental trials were run once on each fish (i.e. sample size for each response was $N = 12$ for captive-bred and $N = 14$ for wild-caught). The trials were Control (no threat) and Vision (visual contact with the predator). These trials were conducted in two rectangular experimental tanks (60 \times 31 \times 24 cm) filled with heated dechlorinated water. A video camera connected to a large television was placed in front of the short side of the experimental tank during the procedures. The tank and the camera were covered with fabric sheets. This isolated the fish from any external disturbance, but still allowed observation of the response through the camera. Duration of the responses of the angelfish was recorded with a stopwatch. After each trial, experimental tanks were drained and cleaned.

Each fish underwent one trial per day. The sequence of trials was randomly assigned by draw for each fish to eliminate potential carryover effects. In all trials, fish were moved into the experimental tank with a net and left for 1 h to acclimate and re-establish normal behaviour. For the sake of this experiment, we considered a pause to be when a fish was motionless for more than 5 s. Any type of motion performed after a pause (rotation or translation) marked the end of the pause.

Control trial

Fish were observed for 10 min under normal, stimulus-free conditions. Duration of the longest pause (maxpause) was recorded. We also observed common activities the fish performed in these conditions. This description was used to identify when fish resumed normal behaviour in the visual trial, as some studies have shown this variable to be affected by the presence of threat (Brown et al., 2009). Normal behaviour was indicated by the fish pecking on the bottom of the tank or at the surface of the water in search of food (feeding), or by continuous swimming along the entire extent of the experimental tank with no intermittent pauses (swimming).

Vision trial

The short side of the experimental tank was placed facing the short side of the JD tank. A partition was used to separate visually the two tanks before positioning them together to avoid visual contact between the fish prior to the beginning of the treatment. After the acclimation period, the partition was removed, which caused both fish to pause. The pause duration of the angelfish was recorded as 'partition-shock'. Afterwards, both fish resumed activity, usually one preceding the other. The angelfish needed the JD moving in their field of vision to initiate another pause. We recorded the duration of this pause as the response of the angelfish to seeing the JD (JDpause). We also recorded the duration until the angelfish resumed motion and launched the first swim towards JD to investigate the risk (firstinvest). Finally, we recorded the time taken to resume normal behaviour (normal).

Statistical analyses

Statistical analyses were conducted using S-plus 8.0. One-way and multivariate analyses of variance (ANOVA and MANOVA, respectively) were run on normal and homoscedastic data. Log ($x + 1$) transformation fixed issues of normality and homoscedasticity for 'JDpause'. The remainder of the variables either fulfilled the assumptions untransformed or were analysed using the non-parametric equivalent Wilcoxon rank-sum test.

Results

In all trials, fish paused after the presentation of the visual stimulus. This pause was interrupted with intermittent motion. The fish would either go forward, backward, or rotate in place with < 5 s pauses between movements. Normal behaviour was resumed when this motion became continuous and traits of normal behaviour (swimming, feeding) were displayed. This occurred after (regardless of fish type) an average of 16 min in the presence of JD for the vision trials.

In the control trial, although wild fish tended to pause for longer compared to captive fish, the difference in 'maxpause' was not statistically significant (means and SE: captive: 6.9 ± 1.7 s, wild: 13.9 ± 4.2 s; Wilcoxon rank-sum, $\chi^2 = 2.17$, d.f. = 1, $P = 0.14$). In the vision trial, the whole model MANOVA run with all four variables was marginally significant ($F = 2.72$, d.f. = 18, $P = 0.06$). Therefore, we decided to run ANOVAs or non-parametric Wilcoxon rank-sum tests for the individual variables. There were significant differences between wild and captive fish for 'normal' and 'JDpause', and a marginally significant difference for 'partitionshock' (Table 1). Wild fish tended to pause longer after the partition was removed, but displayed shorter pauses after detecting JD and faster resumption of normal behavior. There was no difference in the time taken to begin inspections of JD between the two fish groups (Table 1).

Discussion

Surrounding environments and early experiences affect learned and innate behaviours of animals (Huntingford, 2004). They cause changes in the way animals forage, reproduce, and respond to predators (De Azevedo and Young, 2006; Kelley et al., 2006; Orlov et al., 2006). Differences in the anti-predator behaviour of wild-caught and captive-bred animals have

intrigued behavioural ecologists as well as conservation biologists. In our study, we compared the reaction of captive-bred and wild-caught angelfish to visual stimuli from a predator. We did not detect differences in the normal behaviour of the fish in control trials or in the time taken for the angelfish to inspect the predator in the vision trials. However, wild fish tended to pause longer than captive fish in response to a novel stimulus (the removal of a partition), but displayed shorter pauses in response to seeing the predator. Wild fish also resumed normal behaviour faster.

In the control trials, wild fish paused for the same duration as captive fish. Similarly, wild fish paused for the same duration as captive fish upon the removal of the partition in the vision trials. Similar tendencies were recorded by Salonen and Peuhkuri (2006), who found that hatchery-reared European grayling (*Thymallus thymallus*) stopped their aggressive behaviour for the same duration as wild grayling after the movement of a black rubber glove overhead.

Removing the partition between the tank containing the predator and the experimental tank provided the angelfish with a visual stimulus of a live potential predator. Such an approach has been shown to be a stressful predatory stimulus eliciting anti-predator behaviour in zebrafish (*Danio rerio*; Barcellos et al., 2007), Japanese flounder (*Paralichthys olivaceus*; Miyazaki et al., 2004), and slimy sculpins (*Cottus cognatus*; Chivers et al., 2001), with freezing often being observed (Pettersson and Järvi, 2006; Malavasi et al., 2008). In our experiment, angelfish paused instantly after spotting the JD. There was a significant difference in pause duration between captive and wild fish when the predator was detected, but, surprisingly, wild fish ended their pauses faster than captives. Similarly, wild fish resumed normal behaviour significantly sooner than captives. These results are counterintuitive, as wild animals are expected to be more cautious in the presence of predation risk than captive ones. However, such results have been observed by Oliver et al. (2008), who found that spiny lobsters (*Jasus edwardsii*) raised in the absence of predators tended to reduce their activity significantly more in the presence of a threat than those raised with predators. They labelled such lengthy stagnations as overreactions of predator-naive animals to predatory stimuli due to lack of experience, which would likely fade with repeated encounters. In addition, experiments comparing risk-taking behaviour of fish populations with different predation intensities found bolder responses in fish from sites with higher predation (Fraser and

Table 1

Mean duration of four behaviours of 14 wild and 12 captive freshwater angelfish (*Pterophyllum scalare*) in response to visual contact with a jack dempsey cichlid (*Cichlasoma octofasciatum*), a potential predator. Also provided are statistical tests employed to analyse those responses as well as F or χ^2 values, degrees of freedom (d.f.), and significance of results

Variable	Mean \pm 1SE		Statistical test	F/χ^2 value	d.f.	Significance
	Captive	Wild				
Partitionshock: Pause following removal of partition between angelfish tank and that of the potential predator (log-transformed)	0.55 ± 0.12	0.85 ± 0.09	ANOVA	$F = 3.98$	1	$P = 0.06$
JDpause: Pause following detection of potential predator by the angelfish	22.20 ± 14.34	19.61 ± 4.82	Wilcoxon-rank sum	$\chi^2 = 5.25$	1	$P = 0.02$
Firstinvest: Time until first investigation of potential predator by the angelfish	8.08 ± 1.58	8.38 ± 1.90	ANOVA	$F = 0.01$	1	$P = 0.90$
Normal: Time to resume normal behaviour	20.09 ± 1.76	12.23 ± 1.98	ANOVA	$F = 8.44$	1	$P = 0.01$

Gilliam, 1987; Brown et al., 2005). This was observed in experiments of food acquisition or refuge use. More time spent in refuge implies less time spent foraging or reproducing. This incurs costs and fitness disadvantages, especially with persistent predation risks. Thus, bolder individuals that can increase their chances of foraging and reproducing in spite of the presence of predation risks can be selected (Brown et al., 2005).

In terms of investigatory trips towards the predator, we found no significant difference between wild and captive fish. Other experiments investigating this variable found conflicting results. Although some found that captive fish launched inspections sooner than their wild counterparts (Salonen and Peuhkuri, 2006), others found no differences (Malavasi et al., 2004; Sundström et al., 2004), suggesting that this behaviour is not as influenced by experience and rearing environments as the other anti-predator behaviours (Malavasi et al., 2004).

Future research could be improved based on the findings from our study. Larger sample sizes would have afforded us more statistical power. Our small sample size may be responsible for the lack of significance in the 'maxpause' and 'partitions shock' variables. Post hoc power analyses revealed that, given the observed effect sizes, statistically significant differences would have been obtained with sample sizes twice as large as the ones we employed. In addition, using a confirmed predator of the angelfish would eliminate the doubt that angelfish may be naive to the JD. However, we believe this is very unlikely given the overlap in the distributions and habitat of both species, as well as the differences in the responses to the JD we documented (JDpause). Also, more information on the captive breeding conditions, such as the holding densities and generations in captivity, could help explain some of the results as breeding conditions can vary between hatcheries. Moreover, quantifying the proximity and frequency of the investigatory trips to the predator in addition to the duration to start inspections would be beneficial (Brown and Dreier, 2002; Kelley et al., 2005). Finally, a logical extension to this study would be a survival test. Comparing the survival rates of the two fish groups after recording the differences in predator avoidance would allow to determine the survival benefits of the observed differences, and would help qualify those differences as adaptive or maladaptive.

In conclusion, the results lend support to differences in behaviour of wild-caught and captive-bred fish. We found evidence for the effect of rearing environment on the behaviour of fish. Studying the behaviour of captive and wild animals is of importance to conservation biology. Captive-bred animals often exhibit higher risks of predation in wild environments due to their domesticated behaviour. A realistic rearing environment that provides experience with natural threats is required if behavioural differences between captive-bred and wild-caught fish are to be avoided.

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