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Research Article

Differences in anti-predator behavior and survival rate between hatchery-reared and wild grass carp (*Ctenopharyngodon idellus*)

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Abstract – Grass carp *Ctenopharyngodon idellus*, is the primary freshwater species produced in China. Because natural populations have shrunk in the wild, restocking programs using hatchery-reared fish have emerged. Artificial rearing could affect fish anti-predator behavior, thus decreasing their survival in the wild. The impact of artificial rearing on *C. idellus*'s behavior remains unknown because empirical studies are scarce. In this study, we compared anti-predator behavior and survival rate between hatchery-reared and wild *C. idellus*. Both hatchery-reared and wild *C. idellus* displayed clear anti-predator behavior when exposed to visual and odor cues of a predator. However, hatchery-reared *C. idellus* showed significantly lower aggregation index (reflecting shoaling behavior), inspection rate and spent less time in risky area compared to their wild counterparts. When directly exposed to predators, more hatchery-reared *C. idellus* were predated. This raises concerns about the efficiency of restocking programs and highlights the need to adjust artificial rearing and stocking conditions of *C. idellus* to produce fish that are better adapted to natural conditions.

Keywords: hatchery fish / anti-predator behavior / survival rate / restocking

1 Introduction

The grass carp *Ctenopharyngodon idellus* (Valenciennes), is a fish species of the *Cyprinidae* family native to Eastern Asia (Guillory and Gasaway, 1978). Adult individuals can be found in lakes, ponds, pools, and the backwaters of large rivers (Shireman and Smith, 1983). It prefers large, slow-flowing, or standing water bodies and tolerates temperature ranging from 0 to 38 °C (Froese and Pauly, 2017). It is a typical herbivorous species worthy of commercial cultivation because of its proficiency in consuming phytoproteins and carbohydrates (Wang, 2000; Froese and Pauly, 2017). As one of the major freshwater species in the Yangtze River, its production accounted for 25% of all freshwater fish production in 2011 in China. The natural resources of *C. idellus* were abundant in the Yangtze River before the 1960s (Liu *et al.*, 2004), but water pollution, habitat degradation, and over-exploitation have caused wild fish resources to decline sharply since the 1990s (Gui, 2003). Since 2002, an annual program for supplementing *C. idellus* was implemented in the Yangtze River to restore and maintain this fish resource, but the potential consequences remain unknown.

Hatchery-based restocking programs are well known and widely implemented worldwide to conserve wild fish populations (Fraser, 2008; Kostow, 2009). It is estimated that over 300 fish species were released worldwide every year (Welcomme and Bartly, 1998). Although habitat restoration should always be the first choice when possible, rearing fish in hatcheries and releasing them into the wild can be useful in maintaining sensitive natural populations along with sustainable fish production (Einum and Fleming, 2001; Araki *et al.*, 2007; Johnsson *et al.*, 2014). As young fish that enable to survive the early stages of life are also likely to survive to adult size, many endangered species recovery programs rely on the release of hatchery-reared individuals to ensure long-term population viability (Brown and Day, 2002).

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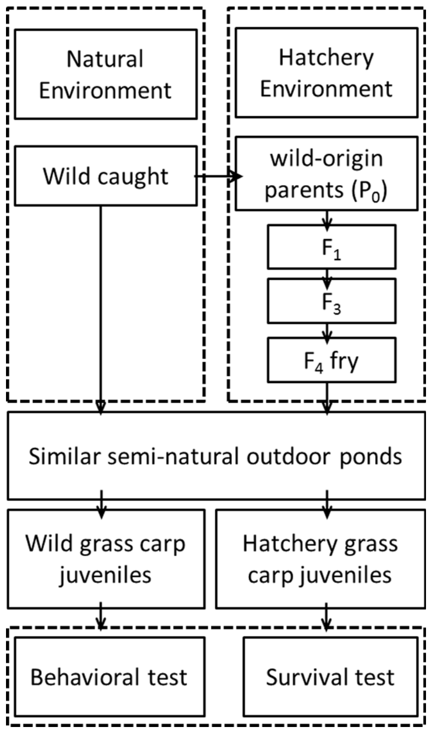


Fig. 1. Overview of the experimental design. Wild-caught and hatchery-reared fish originated from the same region of the Yangtze River, between Honghu (114.02 E; 30.08 N) and Huangang (114.87 E; 30.45 N). Hatchery-reared fry were kept in hatchery conditions for 3 generations. Wild-caught and hatchery-reared F_4 fry were kept in outdoor ponds until they became juveniles, at which point they were transferred to indoor tanks for acclimation (two weeks) before experimentation.

Although hatchery rearing techniques are progressing, hatchery-reared fish often display behavioral deficits and suffer high post-release mortality rates in the wild (Brown and Day, 2002). Indeed, behavioral traits in particular are modified by hatchery conditions. Fish living in the natural environment are exposed to complex habitats and natural challenges (Armstrong *et al.*, 2003). In contrast, hatchery conditions eliminate potential stressors and modify the experiences and learning conditions of reared fish. Matsuzaki (2009) and colleagues found that feral strains of the common carp *Cyprinus carpio* (Linnaeus) behave differently to domestic strains. Of the two, the feral strains are better at detecting prey and are more cautious of predator attacks (Matsuzaki *et al.*, 2009). Apart from altering behavior, hatchery programs have been documented to impact the genetic and ecological structure of wild *C. idellus* (Liu *et al.*, 2009; Zhao *et al.*, 2011).

Considering hatchery shortfalls, Chinese fisheries scientists have had concerns about the potential impacts of stocking programs on fish conservation for more than a decade (Shen, 2002; Chen, 2003; Gui, 2003). A great number of studies have investigated the impacts of hatcheries on salmonids' behavioral traits. By comparison, studies of cyprinids are scarce, especially those focused on *C. idellus*, despite its considerable biological and economic importance.

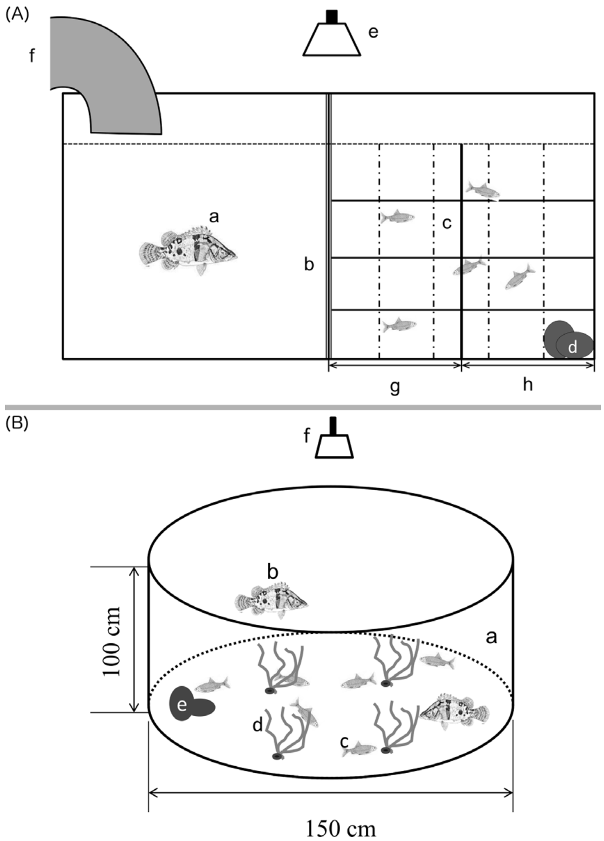
In this study, we compared the behavioral responses of hatchery-reared and wild *C. idellus* to predators after visual and olfactory contact. We also compared their survival rate after being placed in contact with an actual predator. With this study, we hope to shed light on potential ecological risks caused by hatchery-reared *C. idellus* in stocking programs and to improve hatchery conditions to better match natural conditions.

2 Material and methods

2.1 Experimental fish

In this study, hatchery-reared ($n = 160$) and wild ($n = 160$) *C. idellus* were used. Wild *C. idellus* fry were caught in the Yangtze River in China (Honghu, Wuhan; 114.02 E; 30.08 N) using floating trap nets. Fry were collected instead of juveniles because wild *C. idellus* juveniles are sparse in the Yangtze River, making it difficult to catch enough juveniles for this study. Hatchery-reared *C. idellus*, F_4 generation, were obtained from a local hatchery. Ancestors (P_0) of hatchery-reared fish were wild *C. idellus* caught from the Yangtze River ranging from Honghu (114.02 E; 30.08 N) to Huanggang (114.87 E; 30.45 N). The ancestors' offspring (generations F_1–F_4) were hatchery-reared (Fig. 1). The F_1 generation was directly obtained from 60 to 80 pairs of wild brood fish. These brood fish were selected from more than 1000 wild-caught P_0 *C. idellus.* About 1000 F_1 individuals were reared to maturity in captivity, and 60–80 pairs of F_1 were then selected as brood fish for F_2. Analogously, the F_3 and F_4 generations were acquired. This rearing method obtained hatchery-reared F_4 individuals with great genetic diversity (Wang, 2000). In the hatchery, brood fish (10–15 kg in body weight, 300–450 ind·ha^{-1} in density) were reared in ponds 1.5–2.0 m in depth, and the female:male ratio was 1:1.2. On a daily basis, they were provided with commercial feed, aquatic plants (common duckweed *Lemna minor*), wheat seedlings, and vegetables. Artificial reproduction began when the water temperature rose to 23–26 °C, between April and June. Brood fish were injected with luteotropin releasing hormone analogue at 10 μg·kg^{-1} for females and 5 μg·kg^{-1} for males. Oocytes were fertilized using the dry method for 2 min. The fertilized eggs were then transferred to the fry incubator for 4–5 days until hatched.

Both hatchery-reared F_4 fry and wild fry were then transferred into respective outdoor ponds in similar conditions. The fry were reared at a density of 50 ind·m^{-2}, and they fed primarily on natural zooplankton during the early phase (30 days) of culture. During the later phase (30 days), artificial food pellets (36.0% protein, 12.1% lipid, 11.3% ash, and 18.2 J·mg^{-1} energy) were provided. After two months, their mean (±S.E.) total length (L_T) was 6.21 cm (±0.02 cm) and mass was 2.35 g (±0.02 g), and they were transferred to indoor tanks for acclimation. The two groups of juveniles were kept separate in circular fiberglass tanks (φ, 150 cm; volume, 1766 L) with a water recycling culture system. The tanks were filled with gravel and plants to minimize stress. During acclimation, water temperature was maintained between 25.0 and 27.5 °C under a 12-h light (daytime), 12-h dark (night) cycle. They were fed commercial food pellets (36.0% protein, 12.1% lipid, 11.3% ash, and 18.2 J·mg^{-1} energy) twice daily.



Q2 **Fig. 2.** Test tanks for measuring anti-predator behavior (100 × 30 × 40 cm; A) and for survival rate with exposure to a predator (B). The former containing (a) predator mandarin fish; (b) a transparent partition; (c) a compartment containing 5 wild or hatchery-reared *C. idellus* selected at random; (d) gravel shelter; (e) light source, and (f) fixed tube used to introduce a predator. The tank was divided into a risky area (g) and a non-risky area (h). The latter containing (a) test tank (φ, 150 cm; H, 100 cm); (b) two predator mandarin fish; (c) 10 wild and 10 hatchery-reared *C. idellus* selected at random (size-matched); (d) aquatic plant shelter; (e) gravel shelter; and (f) light source.

2.2 Anti-predator behavioral experiment

Pair-contrasts methods were performed to compare the anti-predator behavior of hatchery-reared and wild *C. idellus* in the presence of mandarin fish *Siniper cachuatsi* (Basilewsky), a natural enemy that is common and widely distributed in the Yangtze River and lakes along the river (Liang *et al.*, 1998). Samples of hatchery-reared ($n = 40, L_T = 7.62 \pm 0.04$ cm, mass = 3.69 ± 0.08 g) and wild ($n = 40, L_T = 7.67 \pm 0.05$ cm, mass = 4.11 ± 0.09 g) *C. idellus* were randomly selected and tested, and no significant difference was found for L_T (*t*-paired test, $P > 0.05$) between the two groups. Eight paired-test trials were conducted wherein the behavior of five hatchery-reared and five wild *C. idellus* were tested. Predators ($n = 8, L_T =$ 26.9 ± 5.1 cm, mass = 315.4 ± 29.8 g) were captured in Liangzi Lake using trap nets. Prior to the experiment, eight predators were reared under the same condition as that used to acclimate *C. idellus*. The test tank (100 × 30 × 40 cm, Fig. 2A) was filled with dechlorinated water (120 L). A transparent perforated Plexiglas™ partition was used to divide the tank into two equal compartments. The partition allowed visual and odor cues to be exchanged between the two species. One compartment contained a predator and the other five *C. idellus* (either hatchery-reared or wild). The compartment containing *C. idellus* was divided into eight cells, each 25 × 10 cm in size (Fig. 2A). It was also divided into two equal parts marked by a vertical line on the back wall of the tank. The part closer to the partition was defined as a risky area while the other part, containing two stones, was defined as a non-risky area (Fig. 2A). The compartment chosen to contain the predator was alternated on a daily basis to avoid spatial biases (Duan *et al.*, 2013). Additionally, the individual predator used for testing was changed regularly to avoid potential biases caused by activities unique to individuals. The rear and lateral walls of the tank were covered by black sheets to reduce visual disturbances and facilitate video-tape analysis. An 80-W lamp illuminated the tank above the water. The lighting regime was maintained as in the acclimation period, and the water temperate, dissolved oxygen, and pH were 25 ± 0.5 °C, $7.5 \pm 0.4\ \mathrm{mg \cdot L^{-1}}$, and 8.19 ± 0.2, respectively.

All trials were carried out between 1000 and 1400 h every day. Each trial consisted of a paired comparison that included two test tanks, one with five randomly-selected hatchery-reared *C. idellus*, and one with five wild *C. idellus*. The *C. idellus* were introduced and acclimatized for 2 h. Their behavior was subsequently filmed for 1 h using a video camera (HDR-PJ790E; Sony). Then, a predator was introduced through a sliding tunnel (Fig. 2A), and filming continued for another hour. The sliding tunnel was fixed and extended from the outside of the tank to the surface of the water inside (Fig. 2A). This allowed introduction of the predator with minimal disturbance to the *C. idellus*. Once a trial was completed, all *C. idellus* and the predator were transferred to other holding tanks. The test tank was then prepared for reuse by deep cleaning and refilling with fresh water to remove potential alarm odor cues.

Because fish movement along the third dimension (from tank front to back) was not filmed, only two-dimensional images were analyzed. Videos taken from 5 min before to 5 min after predator introduction were analyzed. A frame was extracted every 20 s from each 5-min period, yielding 15 temporal frames per period. Three indicators reflecting axes of anti-predator behavior were measured, finding the mean (±S. E.) for each 5-min period for each group in each trial.

One indicator was the time spent in the risky area, reflecting the sensitivity of prey in detecting and collecting information about predators (Magurran and Seghers, 1990; Murphy and Pitcher, 1997). Another indicator was shoal cohesion, measured using the dispersion index (I_D), calculated as the ratio between the variance and the mean of the distribution of individuals in a defined area (Malavasi *et al.*, 2004). For every temporal frame, fish were counted in each of the eight cells so that the mean and variance of the fish distribution across the cells could be determined. A completely random dispersion is when $I_D = 1$. When $I_D > 1$, regular aggregation of the shoal is indicated. Finally, inspection rate was measured. During an inspection event, *C. idellus* maintains visual contact with the predator and positions itself facing the predator while slowly swimming (Seghers, 1973, Kelley *et al.*, 2003). Of the five *C. idellus* in the tank, those displaying this behavior as inspection rate were counted.

Table 1. Effects of predator exposure (before and after exposure) and origin (wild or hatchery) on anti-predator behavior of grass carp (mixed models with fish group as a random effect).

Responding variables		Predator exposure	Origin	Predator exposure × origin (interaction)
Time spent in risky area	DF	485	485	485
	T	26.88	6.30	−3.08
	P	<0.001	<0.001	0.002
Shoal cohesion	DF	485	485	485
	T	−2.34	3.75	−0.39
	P	0.020	<0.001	0.690
Inspection	DF	485	485	485
	T	5.22	10.09	−6.75
	P	<0.001	<0.001	<0.001

2.3 Predation experiment

Paired-contrasts methods were performed to compare anti-predator ability between the hatchery-reared and wild *C. idellus*. Four circular fiberglass tanks (φ, 150 cm; height, 100 cm; water depth, 80 cm) were supplied with temperature-controlled, flow-through water, and the floors were covered with gravel and aquatic plants. Two mandarin fish of similar size ($L_T = 29.4 \pm 3.9$ cm, mass $= 395.9 \pm 22.3$ g) were introduced in the tank and were allowed to prey on *C. idellus*.

Hatchery-reared ($n = 120$) and wild ($n = 120$) *C. idellus* were selected for the tests. Because the size of the individual is a key factor affecting a fish's chance of survival (Nilsson and Brönmark, 1999), the *C. idellus* were divided into two groups. The big-sized group weighed 7.97 g (±0.05 g) and measured 9.67 cm (±0.01 cm) in length (*t*-paired test of L_T, $P > 0.05$), and the small-sized group weighed 1.95 g (±0.01 g) and measured 5.86 cm (±0.01 cm) in length (*t*-paired test of L_T, $P > 0.05$). Six replicate trials were conducted for both groups, and each trial included 10 hatchery-reared and 10 wild fish. Feeding was suspended for all individuals (predators and prey) 24 h before each trial. Hatchery-reared *C. idellus* were marked by clipping a small part of the right ventral fin; wild fish were similarly marked on the left ventral fin (Zhang *et al.*, 2014). Each trial started when size-matched hatchery-reared ($n = 10$) and wild ($n = 10$) fish were introduced *via* a net cage to a circular tank for 30 min acclimation. The net cage was then removed to expose the *C. idellus* to the predators. The trial terminated when approximately 50% of the *C. idellus* were eaten by the predator, then the remainder was counted (Zhang *et al.*, 2014). The survival rate, was calculated as S/10 100, where S is the number of surviving fish.

2.4 Statistical analyses

To compare the anti-predator behavior of hatchery-reared *vs.* wild *C. idellus*, linear mixed-effects models in the R package "nlme" (Crawley, 2007) were used to account for the non-independence of repeated measures taken on the same group of fish before and after predator exposure (Zuur *et al.*, 2009). The three anti-predator behavior indicators were the response variables. Group identity was included as a random factor. Fixed effects were fish origin (wild or hatchery), time relative to predator exposure (before or after), and their second-order interaction. The fish were size-matched, eliminating size from the model. When a significant interaction between the origin and time of exposure was found, *post hoc* mixed models were applied separately before and after predator exposure. The significance threshold was 0.05.

To compare the survival rate of hatchery-reared and wild *C. idellus* in the predation experiment, the generalized linear mixed-effects model from the "lmer" package was used. This model can evaluate the random effect of fish group, the fixed effects of origin and size, and their second-order interaction. Using this model, the effects of origin and total size on survival rate (binomial distribution) were tested. All data were analyzed using R (R Development Core Team).

3 Results

3.1 Anti-predator behavior

Hatchery-reared and wild *C. idellus* avoided the risky area differently, as shown by the significant origin-by-exposure on the time spent in the risky area (Tab. 1, $P < 0.01$). *Post hoc* tests showed no difference in avoiding the risky area before predator exposure ($P = 0.089$), but avoidance of the area was stronger for hatchery-reared fish compared to wild fish after predator exposure ($P < 0.001$, Fig. 3a).

Hatchery-reared and wild *C. idellus* changed their shoaling behavior in the same way after predator exposure, as indicated by the non-significant origin-by-exposure (Tab. 1; $P = 0.69$). Fish shoals were more aggregated after predator exposure (Tab. 1; $P = 0.02$; Fig. 3b). Specifically, hatchery-reared fish aggregated less than the wild fish both before and after predator exposure (Tab. 1; $P < 0.001$, Fig. 3b).

Hatchery-reared and wild *C. idellus* changed their inspection rate differently after predator exposure, as shown by the significant origin-by-exposure (Tab. 1; $P < 0.001$). *Post hoc* tests showed that wild fish increased their inspection rate after exposure to the predator, but hatchery-reared fish reduced them after predator exposure (before predator exposure, $P = 0.70$; after predator exposure, $P < 0.001$, Fig. 3c).

3.2 Survival rate

C. idellus of different body sizes had similar survival rates (effect of length, $z = 0.38$, $P = 0.70$), but wild fish survived better than hatchery-reared fish when directly exposed to the predator (effect of origin on survival rate, $z = 3.71$, $P < 0.001$; Fig. 3d).

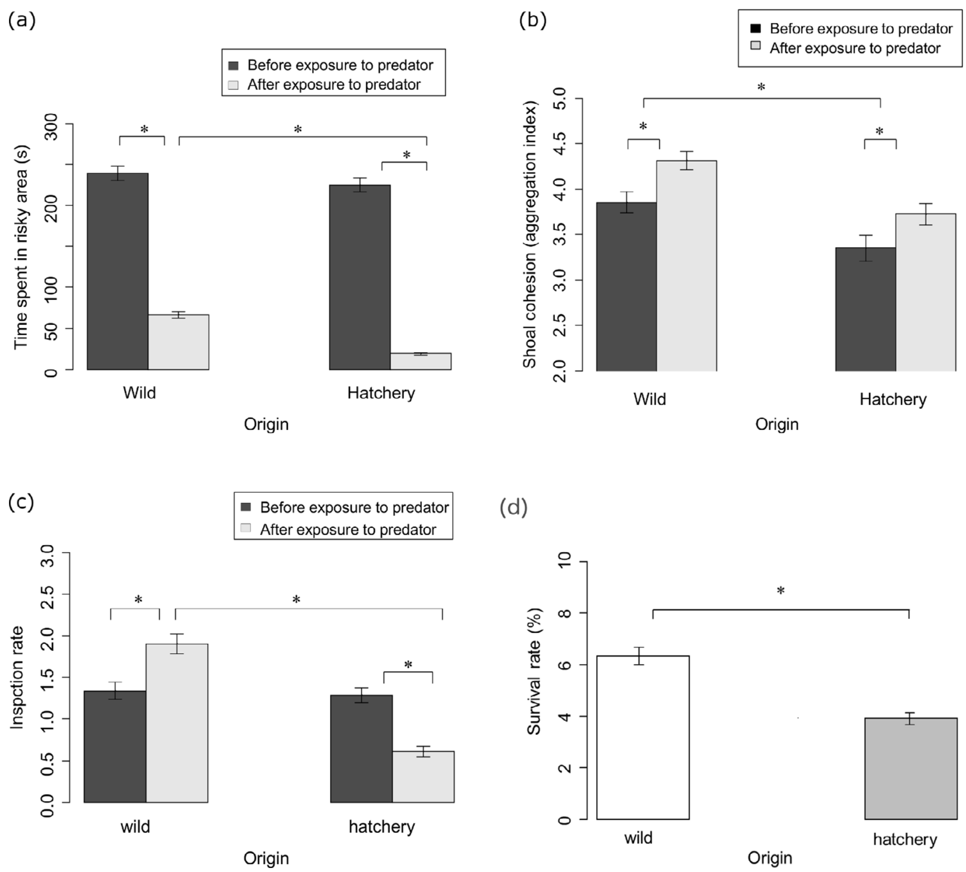


Fig. 3. Comparisons of indicators measured in the anti-predator behavioral experiment. (a) Mean (±S.E.) time spent in the risky area by wild and hatchery-reared fish across eight replicates ($n = 5$ fish per trail). (b) Mean (±S.E.) shoal cohesion (aggregation index) of wild and hatchery-reared fish across eight replicates. (c) Mean (±S.E.) inspection rate (number of fish facing the predator) of wild and hatchery-reared fish across eight replicates. Asterisks above bars indicate significant differences ($P < 0.05$) after *post hoc* tests. (d) Mean (±S.E.) survival rate of wild and hatchery-reared fish after a predation event across six replicates. Asterisks above bars indicate significant differences ($P < 0.05$) between groups.

4 Discussion

Taken together, these results suggest that hatchery-reared *C. idellus* retained some anti-predator abilities, consistent with previous experimental studies of other species, such as cod *Gadus morhua* (Linnaeus), European sea bass *Dicentrarchus labrax* (Linnaeus), and guppies *Poecilia reticulata* (Peters) (Malavasi *et al.*, 2004; Meager *et al.*, 2011; Swaney *et al.*, 2015). However, hatchery-reared *C. idellus* displayed lower shoaling and inspection behavior when exposed to predator cues compared to wild fish, suggesting their anti-predator behavior is less efficient than their wild counterparts. Accordingly, hatchery-reared *C. idellus* had a lower survival rate than wild fish when exposed to an actual predator.

In addition, hatchery-reared *C. idellus* were more cautious in the risky area than wild fish. Such risk-averse behavior was also documented in hatchery-reared *D. labrax* and *G. morhua* (Malavasi *et al.*, 2004; Nordeide and Svasand, 1990). To our best understanding, behavior of the hatchery-reared *C. idellus* observed in this study have not been observed in other studies of carp. Wild *C. carpio* were usually reported to be more cautious to predator cues, compared with its domestic counterparts (Matsuzaki *et al.*, 2009). However, studies using carp still remain scarce, and further explorations of the mechanisms underlying behavioral divergence are required in the future.

Hatchery-reared *C. idellus* displayed lower shoaling cohesion and inspection rate than their counterparts in this study. In general, group formation is a widespread phenomenon in animal populations. This is thought to be an efficient defense strategy against predators (Krause and Ruxton, 2002). Prey shoals are reportedly rarely attacked by bluegill sunfish *Lepomis macrochirus* (Rafinesque) because the predator prefers individuals that are not in groups (Ioannou *et al.*, 2012). Accordingly, the wild *C. idellus* achieved higher survival rate than hatchery-reared fish when exposed to predators in this study, indicating that wild fish benefited from their good shoaling and inspection rate.

More specifically, more hatchery-reared *C. idellus* were eaten than wild *C. idellus* when exposed to actual predator attacks. This could have resulted from the altered anti-predator behaviors of the hatchery-reared *C. idellus*. Studies of steelhead trout fry *Oncorhynchus mykiss* (Walbaum), and juvenile coral reef damselfish *Pomacentrus wardi* (Bonaparte) demonstrated that fish fed in artificial conditions without predator experience were predator-naive and vulnerable to benthic predators (Berejikian, 1995; Lönnstedt *et al.*, 2012). Predator-naive *D. labrax* juveniles were observed to acquire anti-predator abilities through training with predators (Malavasi *et al.*, 2004). Hence, hatchery-reared *C. idellus* could be trained using complex habitats (*e.g.*, water structures, shelters, live predators) to strengthen their anti-predator abilities in future reintroduction to natural conditions where high predation risks exist.

In this study, only early life conditions (incubation and approximately 10 days after hatching) differed between hatchery-reared and wild fry. The wild fry were kept in the hatchery for two months before the experiment, the domestication could partly influence their response to predator signals. In spite of this, the present study show that wild *C. idellus* outperformed their hatchery-reared counterparts in anti-predator response and survival rate, suggesting that early stage exposure to predators or predator cues in nature could play important roles in behavior divergence. However, we must also acknowledge that bias owing to our experimental design should not be overlooked. The mechanisms underlying the behavioral differences between the hatchery-reared and wild *C. idellus* thus remain to be elucidated in future studies.

5 Conclusion

Compared to wild *C. idellus*, hatchery-reared *C. idellus* exhibited altered anti-predator behavior and lower survival rate when exposed to a actual predator. This suggests that hatchery-reared *C. idellus* could pose potential ecological risks when released in nature for conservation purposes. With this study, we hope to motivate further work on hatchery rearing consequences and to improve success in stocking programs.

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