



Impacts of domestication on angling vulnerability of common carp, *Cyprinus carpio*: the role of learning, foraging behaviour and food preferences

T. KLEFOTH

Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

T. PIETEREK

Inland Fisheries Management Laboratory, Department for Crop and Animal Sciences, Humboldt-Universität zu Berlin, Berlin, Germany

R. ARLINGHAUS

Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany
Inland Fisheries Management Laboratory, Department for Crop and Animal Sciences, Humboldt-Universität zu Berlin, Berlin, Germany

Abstract Domestication in fish selection increases vulnerability to angling. Two common garden-reared genotypes of common carp, *Cyprinus carpio* L., differing in degree of domestication (highly domesticated mirror carp and less domesticated scaled carp) were exposed to fishing in two environments (i.e. ponds and laboratory tanks) to quantify vulnerability to angling. Foraging behaviour and food preferences were quantified to explain variation in angling vulnerability in a mechanistic manner. Domesticated mirror carp were more vulnerable to angling gear than scaled carp in both environments, which was related to greater food intake and bolder-foraging behaviour. Independent of genotype, catchability decreased and time until first capture increased over fishing time, indicating learned hook avoidance. No differences were observed in food preferences among genotypes, rendering bait-selective feeding an unlikely explanation for differential vulnerability to angling. It was concluded that vulnerability to angling has a genetic basis in carp and that boldness plays a paramount role in explaining why more domesticated genotypes are more easily captured by angling.

KEY WORDS: adaptation, catchability, common garden, fisheries-induced evolution, hook avoidance, social learning.

Introduction

Predator–prey relationships like those between anglers and their target fish are regulated by the fish's antipredator behaviours (Cox & Walters 2002; Van Poorten & Post 2005; Askey *et al.* 2006). Antipredator behaviour in fish has a genetic basis (Seghers 1974; O'Steen *et al.* 2002; Ghalambor *et al.* 2004), but experience and learning over time can strongly influence the development of

antipredator responses (Kieffer & Colgan 1992; Kelley & Magurran 2003; Griffin 2004). The propensity of fish to learn from experience has been found to be higher in fish adapted to high-predation environments than fish adapted to low-predation environments (Huntingford & Wright 1992), indicating that not only antipredator behaviour *per se*, but also the ability to learn, has an evolutionary basis. Therefore, a different degree of adaptation to natural predation risk might also influence

Correspondence: Thomas Klefoth, State Sport Fisher Association of Lower Saxony (Landessportfischerverband Niedersachsen), Bürgermeister-Stümpel-Weg 1, 30457 Hannover, Germany (e-mail: t.klefoth@lsfv-nds.de)

responses of fish towards baited hooks in recreational fisheries.

Management of freshwater recreational fisheries often involves stocking activities using fish raised in captivity (Pearsons & Hopley 1999; Arlinghaus *et al.* 2002). Therefore, individual fish of the same species and within the same water body can substantially differ in their local adaptation towards predation risk, because phenotypic traits related to risk-taking are often altered by the domestication process within fish hatcheries in ecological or evolutionary contexts (Price 1999; Huntingford 2004; Sundström *et al.* 2004). The combination of selective breeding and early life experiences of unnaturally low-risk conditions within culture facilities strongly shapes fish behaviour (Price 1999). As a consequence of the domestication process, cultured fish can be assumed to represent the risk-taking end of the behavioural spectrum (Huntingford 2004). Fish raised under culture conditions are thus usually more vulnerable towards angling than their wild conspecifics as has been shown for a variety of salmonids [brook char, *Salvelinus fontinalis* (Mitchill) (Flick & Webster 1962); cutthroat trout, *Oncorhynchus clarkii* (Richardson) (Dwyer 1990); rainbow trout, *Oncorhynchus mykiss* (Walbaum) (Dwyer & Piper 1984); brown trout, *Salmo trutta* L. (Mezzera & Largiadèr 2001)]. Similarly, differences in angling vulnerability between high- and low-domesticated genotypes of omnivorous common carp, *Cyprinus carpio* L., have been reported where domesticated mirror carp were more readily captured by passive angling tactics than their less domesticated, scaled conspecifics (Beukema 1969; Raat 1985). However, little is known about the specific traits that render more domesticated genotypes more vulnerable to angling, although boldness behaviour is likely to play an important role (Klefoth *et al.* 2012). In addition, preferences for artificial food (such as purposely made baits or corn kernels in carp fishing, Niesar *et al.* 2004; Rapp *et al.* 2008) or ability to digest carbohydrate-rich cereals, to which domesticated fish have been ecologically or evolutionarily adapting under farm conditions, may play an important role (Suzuki *et al.* 1978).

In general, the impact of fish learning abilities on angling catch rates has been shown for different predatory species by documenting declining catch rates with increasing fishing pressure in a catch-and-release fishing context [largemouth bass, *Micropterus salmoides* Lacépède (Anderson & Heman 1969; Hackney & Linkous 1978); rainbow trout (Van Poorten & Post 2005; Askey *et al.* 2006); northern pike, *Esox lucius* L. (Beukema 1970a; Kuparinen *et al.* 2010)]. Similarly, omnivorous carp were found to learn from previous capture events insofar as fish that were already captured within a fishing season were found less likely to be caught in the

future compared with previously uncaptured conspecifics (Beukema 1970b; Raat 1985). However, it remains unclear whether differently domesticated fish differ in their ability to avoid being hooked as a consequence of learning. Four issues that are not mutually exclusive are worth noting. First, as domesticated fish might be selected for rapid growth, there might be a corresponding selection for reduced allocation of energy into the building of the neural network leading to reduced cognitive abilities (Mery & Kawecki 2003). Second, the holding of domesticated fish in artificial conditions might reduce the ability of these fish to learn complex tasks (Marchetti & Nevitt 2003). For these two reasons, domesticated fish might express a constantly higher catchability over time relative to less domesticated fish. An alternative perspective is that cultured fish might be initially more vulnerable to angling than less domesticated individuals, but, with increasing experience, differences between the two groups might vanish owing to social learning effects (Beukema 1970b; Krause 1993; Brown & Laland 2003). A final issue is that differences in vulnerability between fish of high and low domestication (and hence adaptation to natural predation risk) might be strongly dependent on the ecological context as a consequence of genotype \times environment interactions (Klefoth *et al.* 2012). Therefore, differences in vulnerability among high- and low-domesticated genotypes might be context dependent.

Another reason for differences in angling vulnerability between fish with differences in their adaptation to culture conditions could be related to food preferences, consumption rate and food-intake speed. Experiments determining differences in the feeding behaviour of wild and domesticated brown trout from the same river showed that wild trout ate more and were quicker to attack and consume prey than domesticated trout (Sundström & Johnsson 2002). Similarly, using differently domesticated carp strains reared in a common garden, Matsuzaki *et al.* (2009) found wild carp to attack prey items more rapidly and to have higher consumption rates than highly domesticated genotypes. However, both studies were based on natural food items. Suzuki *et al.* (1978) used commercial fish pellets and natural worms in trials with carp and found domesticated carp to prefer artificial food over natural food resources and to be more readily captured on the non-natural food. Translating these results into an angling context using baits like worms or maggots, wild genotypes should be more vulnerable to angling than their domesticated counterparts. However, in most contemporary angling for carp, artificial bait items are used such as corn kernels, other seeds or so-called boilies (Niesar *et al.* 2004). Domesticated carp might show a higher consumption rate of this artifi-

cial food, which might be one mechanism for the higher vulnerability of these genotypes using such baits (Suzuki *et al.* 1978).

The objective of this study was to analyse the vulnerability to angling over time and its mechanistic basis as revealed by two genotypes of common garden reared carp (scaled and mirror) with known differences in genetic adaptation to low-risk culture conditions. Tests for angling vulnerability were conducted during day and night in two different environments (i.e. laboratory tanks and ponds) to investigate the influence of the environment and visual cues on threat recognition and learned hook avoidance. Laboratory experiments on foraging activity and preferences of a novel food item were conducted in a two-way-choice experiment to understand some of the mechanisms responsible for differences in vulnerability between the two genotypes of carp. It was hypothesised that more domesticated carp would be more vulnerable overall, and vulnerability would shift to the dark periods with increasing fishing pressure. It was also hypothesised that reasons for the differential vulnerability would be related to increasing consumption rates and a preference for corn kernels as bait among domesticated carp. Finally, wild genotypes were assumed to exhibit greater learning to avoid future capture compared with domesticated carp.

Material and methods

Study animals

Study animals involved two genotypes of common carp differing by distinct scale patterns reflecting its evolutionary history of adaptation to aquaculture conditions as described by Klefoth *et al.* (2012). All carp used were raised at a commercial fish hatchery (Fischzucht Wegert, Ostercappeln, Germany, 52°19'52" N, 8°14'48" E) in the same common garden pond environment. Parental fish descended from two selection lines: (1) a selection line with scaled morphotypes; and (2) a selection line in which scaled morphotypes were previously crossed with strongly domesticated mirror carp selection lines. Fish from both selection lines were stocked into the same common garden pond for reproduction. Young-of-the-year mirror carp could only develop as a result of two breeders from the strain originally crossed with domesticated mirror carp (strain 2) (Kirpichnikov & Billard 1999). All juvenile carp were exclusively fed with standard carp dry food in addition to any natural food ingested in the shallow (1.5 m deep) earthen common garden pond (40 m × 50 m). At an age of 10 months, a subsample of the fish was transported to the Leibniz-Institute of Freshwater Ecology and Inland Fisheries in

Berlin, Germany, for angling experiments, and another subsample was transported to a laboratory at Humboldt-Universität zu Berlin, Germany, for laboratory tests on feeding behaviour and food preferences of the fish. Juvenile carp were chosen as experimental fish because use of much larger and older fish would have been impractical under laboratory conditions. In both locations, fish were kept in tanks (1 m × 1 m × 1 m; 5 fish per 100 L) with tap water in a recirculation system (mean temperature ± SD 18 ± 1.5 °C, exchange rate about once per day). Fish were fed with standard carp pellets (5 mm diameter; Aller Classic, Aller Aqua, Golßen, Germany), and the total daily food amount was approximately 1.5% of fish body wet mass.

Tagging of fish

All carp ($N = 100$ scaled carp and $N = 100$ mirror carp used for angling experiments and $N = 54$ scaled carp and $N = 54$ mirror carp used for laboratory experiments on foraging activity and food preferences) were individually marked with passive integrated transponders (PIT) for individual identification. PIT (23 mm length, 2 mm width; Oregon RFID, Portland OR, USA, 2% tagging mortality) were surgically implanted into the fish's body cavity following the method described by Skov *et al.* (2005). Before PIT implantation, fish were anaesthetised using a 1 mL L⁻¹ of 9:1 solution of ethanol/clove oil in well-aerated water at 18 °C. After PIT implantation, all fish were measured for total length (TL, to nearest mm) and allowed to recover for a minimum of 3 days before experiments started.

Tests for angling vulnerability within ponds

To investigate the vulnerability to angling of scaled and mirror carp under seminatural conditions in ponds, each of three pond replicates (12 m × 5 m × 1 m; L × W × H) was stocked with 40 similar-sized carp (20 scaled carp and 20 mirror carp, mean TL ± SD pond 1: 199 ± 6.9 and 199 ± 12.1 mm, *t*-test, $t = 0.08$, $P = 0.936$; pond 2: 199 ± 4.7 and 200 ± 11.9 mm, *t*-test, $t = -0.26$, $P = 0.797$; pond 3: 199 ± 6.1 and 197 ± 11.2 mm, *t*-test, $t = 0.78$, $P = 0.440$). Fish were allowed to acclimatise for 9 days before angling experiments started. Pond experiments were conducted in September 2008. The ponds were continuously supplied with water from the nearby Müggelsee in Berlin (800 ha; shallow; eutrophic). Inflow into the ponds was about 1 L s⁻¹ unfiltered lake water. The environmental conditions in the ponds were documented using temperature loggers (TidbiT datalogger; Onset, Bourne, MA, USA). Mean water temperature ± SD in the ponds over

the study period was 16.2 ± 1.9 °C (range: 13.9–19.5 °C). The ponds contained a shelter structure (2 m × 5 m) made out of black plastic material just above the water surface next to the water inlet, and two pre-defined round angling locations (diameter 0.5 m) at different distances to the shelter (3 and 7 m away from the shelter structure, respectively). Angling was conducted for 20 consecutive days, simultaneously in all three ponds and started 2 h before sunset until 2 h after sunset (total daily angling effort per pond = 4 h). The starting time of daily angling events was alternated every day among the morning or evening twilight periods, and fishing always involved daytime and nighttime periods to estimate the impact of diel period on angling vulnerability. Angling was conducted on the pre-defined angling locations and position of hook placement was alternated between the two locations on a 60-min basis to control for potential feeding location preferences by the study fish. In addition to the baited hook, standard carp pellets (5 mm diameter) were used as pre-baiting food and were provided every 60 min on the feeding locations. Total daily food amount of pre-baiting pellets per pond was 1% of fish body wet mass at the time of stocking (approximately 12 pellets). In addition, for every single pellet, one sweet corn (5–7 mm diameter; Bonduelle, Reutlingen, Germany) was offered, which also served as carp bait on the hook.

Angling and feeding took place simultaneously on the same locations. Sweet corn kernels were used as bait, provided on a bold-rig as described by Rapp *et al.* (2008). This method ensured exclusive shallow hooking of the fish. The hook was connected to a 13-cm multifilament soft leader. The angling equipment consisted of a 3-kg monofilament line, a 15-g sinker, and a short fishing rod (2.1 m, 0.3 lb test curve; Balzer, Lauterbach, Germany). Bites were indicated by an electronic bite indicator (Carp-Sounder Basic VR; Carp-sounder, Germany). After potential self-hooking, the fish was landed quickly using a rubber-net to prevent mucus abrasion (Barthel *et al.* 2003). Fish were then placed into a bucket filled with fresh water for unhooking and PIT identification (Pocket reader; Allflex, Dallas, TX, USA). Afterwards, fish were immediately released in the middle between the two feeding locations. Release of the fish was always conducted within 30 s and no mortality occurred. In addition to the individual ID of captured fish, time of every bite as indicated by the bite indicator was recorded to the nearest 10 s.

Tests for angling vulnerability within laboratory tanks

Additional laboratory-based experiments under controlled environmental conditions were conducted to test for the

consistency of differences in angling vulnerability among the two carp genotypes under fully controlled environmental conditions. This experiment resembled the set-up established in the ponds and used a new set of study animals. This was done to avoid experimental biases based on learning effects of the fish that might have occurred if individuals from the pond environment would have been re-used during laboratory experiments. Experiments were conducted in a large laboratory tank (10 m × 4 m × 1 m; L × W × H) of comparable size with the ponds. The tank was connected to a circulating water system and a biological filter. Water inflow was 2 L s^{-1} and water temperature \pm SD was constant at 22 ± 1 °C. To investigate vulnerability in the laboratory, a total of 40 similar-sized fish (20 scaled carp and 20 mirror carp, mean TL \pm SD 225 ± 20.0 and 229 ± 16.0 mm, respectively, *t*-test, $t = -0.80$, $P = 0.441$) was stocked into the tank and allowed to acclimatise for 9 days before angling experiments started. Laboratory experiments were conducted in March to April 2009. The experiments followed the same protocol described for the pond experiment, with the exception that intervals of changing the fishing locations within the daily 4 h angling periods were 15 min instead of 60 min for logistical reasons. After the 7th day of angling in the laboratory environment, experimental carp were replaced by a new set of 40 fish (20 scaled carp and 20 mirror carp, mean TL \pm SD 224 ± 17.0 and 229 ± 21.0 mm, respectively, *t*-test, $t = -0.89$, $P = 0.377$), and the experiment was replicated.

Foraging behaviour and food preferences of scaled and mirror carp in the laboratory

Behavioural laboratory experiments were conducted in 12 different aquaria of similar size (100 × 40 × 40 cm) to test for differences in feeding behaviour and food preferences between scaled and mirror carp as possible mechanistic explanations for differences in angling vulnerability between the two genotypes. Aquaria were positioned along two walls using metal racks (three tanks abreast and two tanks stacked) in different distances to a window (2 and 4 m). All aquaria were connected to an independent circular filtering system along each wall. Each tank was equipped with a flat metal rail placed at the bottom to divide aquaria visually into a similar-sized left and right compartment, without influencing activities of fish swimming between the two compartments. Focal fish (mean TL \pm SD of scaled carp 230 ± 25 mm and mirror carp 237 ± 30 mm, *t*-test, $t = 1.1$, $P = 0.35$) consisted of individuals from the same common garden as those individuals used for angling experiments. Individuals were randomly assigned

to one of the aquaria and allowed to acclimatise for 7 days. Water temperature within the aquaria was 19.7 ± 1.2 °C. During acclimatisation, fish were fed pellets (same as previously) with an amount of approximately 1% of body wet mass per day, except for the day before observations started, and aquaria were cleaned on a daily basis to remove residual food. Because no food was provided on the last day before the experiments, fish were starved for about 17 h before behavioural observations started.

Focal fish were tested individually for their feeding behaviour and their food preferences for pellet vs sweet corn kernels following an observer-based approach where the observer stood about 3 m away from the aquaria to observe directly behaviour of the fish. During experimentation, the observer provided five items of two different food sources to the fish (five pellets and five corn kernels). Food items (pellets and corn kernels) were similar to those used during angling experiments. The test procedure for food preferences of scaled and mirror carp followed a two-way-choice setup (Holbrook & Schmitt 1988) where the fish had to choose between two different sources of food provided in different areas of the aquaria at the same time. Behavioural variables evaluated were the number of side changes within 10 min after food supply as an indicator of activity during feeding and the time elapsed until first ingestion of a food item. Afterwards, the number of pellets and corn kernels eaten within 10 min and the total sum of food items eaten (maximal 10 food items per replicate) were counted. Behavioural data were replicated three times, and tests for food preferences were replicated six times. Afterwards, the fish in the aquaria were replaced by a new set of focal fish.

Effects of genotype, angling duration and diel period on catchability of carp

Generalised linear mixed models were used to explain the daily absolute number of angling captures within ponds and laboratory tanks. The data set was used to test for differences in the number of captures between scaled and mirror carp (Genotype), the impact of angling duration on captures measured as consecutive fishing days of the experiment (Day) and the diel period at capture on each specific fishing day, distinguishing day and night (Diel period). Diel period was defined as either daytime (period from sunrise to sunset) or nighttime (period between sunset and sunrise). All possible two-way and three-way interactions with Genotype, Day and Diel period were added to the models and subsequently removed if not significant at $P < 0.05$. Pond and tank replicates were added as a random factor to account for inter-repli-

cate variability. In addition, mean daily water temperature was added as a random factor to the model explaining number of angling captures in the pond environment. In all cases, data were not overdispersed and a Poisson error distribution was found to be the best fit to the data. The software package R and function lmer in library lme4 (R Development Core Team 2009) was used for analysis. Variances explained by the models were calculated using Nagelkerke's Pseudo- R^2 .

To investigate the potential for learning ability of the fish as a response towards angling pressure, time until the first capture of the day was regressed on the time until the first bite of the day and on angling duration (defined as the consecutive fishing day of the experiment) using linear regression models. Variance components of pond and tank replicates were low (<1%), indicating minor differences between replicates in the time until the first capture of the day, so that the regressions were calculated using mean values of pond and tank replicates per day. Interaction terms were removed if not significant. One would generally expect the time until first bite and time until first capture of a fish to be positively related. Learning would be indicated by a positive relationship between time until first bite or time until first capture and fishing duration. Moreover, if over time a decoupling of the time elapsed until the first bite and time elapsed until the first capture happens, this would become visible as a non-significant correlation of these variables indicative of learned hooking avoidance over time.

Mechanistic explanations for differences in vulnerability between scaled and mirror carp

Differences in swimming activity during foraging, time to ingest the first food item and the total amount of food items eaten between scaled and mirror carp were tested using linear mixed models. General foraging activity is known to be correlated with boldness, and boldness, measured as foraging activity, differs among mirror and scaled carp (Klefoth *et al.* 2012). Also, genotypes with shorter time to ingest food and greater total food consumption would have a greater likelihood of capture. The dependent variables swimming activity (measured by the number of side changes of the fish while feeding), time to ingest the first food item (measured in seconds) and the total amount of food items eaten were log-transformed to reach normality and homogeneity of variances prior to analyses. The repeated measures design of the experiment (six observations per individual) was accounted for using individual ID as a random factor. Further, position of the aquaria within the wet-laboratory (i.e. close or distant to a window) was added as a ran-

dom variable. Genotype was added as a fixed factor and body size (TL) of the fish was added as a covariate in all models. The interaction of the two fixed predictor variables was insignificant in all cases and deleted for final analyses.

Food preferences of scaled and mirror carp were analysed using paired *t*-tests. The total number of pellets and corn kernels ingested during the experiment was separately compared for both genotypes. Using this approach, differences in food preferences between scaled and mirror carp would become obvious if the paired *t*-tests would indicate a significant preference of one sort of food for one genotype, but not for the other. To quantify the explanatory power of the results, effect sizes *d* for paired *t*-tests were calculated following the approach outlined in Gliner *et al.* (2001) and interpreted as weak ($d \geq 0.2$), medium ($d \geq 0.5$) or strong ($d \geq 0.8$) effects following Cohen (1988).

Results

Effects of genotype, angling duration and diel period on catchability of carp

Within all ponds a total of 19 scaled carp (32%) and 33 mirror carp (55%) were captured over a period of 20 angling days. One individual scaled carp was captured three times, whereas no other scaled carp was captured more than once. Out of the vulnerable pool of mirror carp, eight individuals were caught twice, one individual was captured three times and another individual was

captured four times. The numbers of daily captures within the pond environment were significantly higher for mirror carp than scaled carp (Table 1), and the number of fish caught per day (expressed as a fraction of total stock size, i.e. catchability, in Fig. 1) generally decreased over the course of the experiment (Table 1; Fig. 1). Because interaction terms including genotype were insignificant in all models, this indicated a generally increasing hook avoidance with increasing fishing pressure and angling experience of the fish for both scaled and mirror carp. No effects of diel period on catchability of the fish were observed within ponds in neither of the two genotypes, as indicated by an insignificant Diel period \times Genotype interaction (Table 1).

Similar to the results in the ponds, mirror carp were significantly more vulnerable to capture by angling than their scaled conspecifics under controlled environmental conditions in the laboratory (Table 1). Here, 22 scaled carp (55%) were caught of which three individuals were caught twice, another three individuals were caught three times and a single scaled carp was caught six times. In comparison, 34 mirror carp (85%) were caught in the laboratory experiments, of which 14 individuals were caught twice, four individuals were caught three times and another four individuals were caught four times. The daily number of captures did not only significantly decrease with time spent fishing (Table 1, Fig. 1), but significantly more fish of both genotypes were captured during night, indicating effects of diel period on catchability of the fish within the laboratory. This effect was indicated by a significant Diel period \times Day of angling interaction (Table 1; Fig. 2). The response towards increasing fishing time and time of the day, as measured by the number of daily capture events, did not differ between the two genotypes.

Within the pond environment, a significant positive association between time elapsed until the first bite of the day and time elapsed until first capture was found (Table 2; Fig. 3), and in addition, time until first capture was positively related to the day of fishing (Table 2; Fig. 3). This indicated a behavioural response of learned hook avoidance of carp towards increasing angling-induced risk. Even stronger effects of learned hook avoidance were found within the laboratory where the time elapsed until the first capture of the day was decoupled of the time elapsed until the first bite of the day (Table 2; Fig. 3), while a significant positive relationship between increasing fishing pressure and the time until the first capture of the day persisted (Table 2; Fig. 3). This indicated that fish remained actively foraging at the feeding locations at any time of the experiment, but with increasing fishing effort and duration carp more effectively avoided being hooked during their foraging

Table 1. Generalised linear mixed models to explain the variability of genotype-specific daily angling captures within three replicated ponds and two replicated laboratory tanks based on carp genotype, diel period and consecutive day of angling. Total angling period was 20 days (ponds) and 7 days (laboratory). The models assumed Poisson errors. Pond and laboratory replicates and mean daily water temperature within ponds were considered as random effects. Non-significant interactions were removed from the final models

Parameter	Estimate	SE	Z	P	R ²
Pond					
Intercept	-0.874	0.31	-2.86		0.29
Genotype (mirror)	0.784	0.26	2.98	0.003	
Diel period (night)	0.150	0.25	0.61	0.547	
Day of angling	-0.108	0.02	-4.57	<0.001	
Laboratory					
Intercept	1.867	0.30	6.27		0.69
Genotype (mirror)	0.664	0.21	3.19	0.001	
Diel period (night)	-1.353	0.39	-3.49	<0.001	
Day of angling	-0.535	0.09	-5.76	<0.001	
Diel period (night) \times day of angling	0.449	0.12	3.84	<0.001	

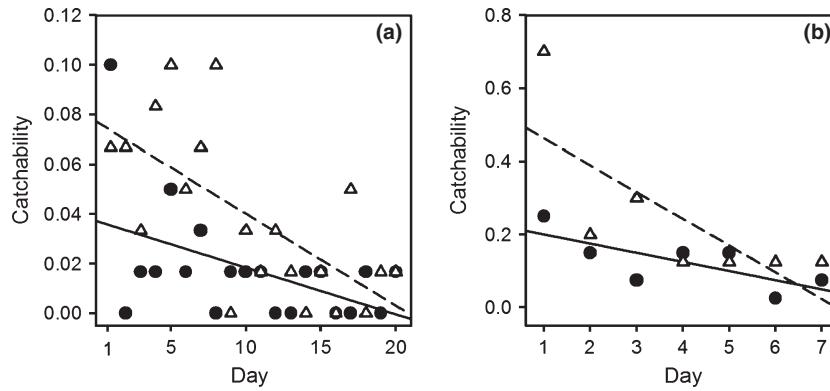


Figure 1. Relationship between the daily catchability (expressed as the total number of fish caught of a given genotype relative to all fish of that genotype) of scaled carp (filled circles, solid line) and mirror carp (triangles, dashed line) and the number of consecutive angling days within ponds (a) and laboratory tanks (b).

activities. This finding was additionally confirmed by visual observations (see Appendix S1 for a video showing active foraging and hook avoidance).

Mechanistic explanations for differences in vulnerability between scaled and mirror carp

Potential reasons for higher vulnerability of mirror carp were derived from the additional behavioural experiments in aquaria. Here, mirror carp were found to be significantly more active during foraging than scaled carp (mean number of side changes within aquaria \pm SD of scaled carp 13.4 ± 2.1 and mirror carp 21.8 ± 1.7 , respectively, linear mixed model, d.f.numerator = 1, d.f.denominator = 107.9, $F = 6.57$, $P = 0.012$). Mirror carp also ingested a higher total amount of food items during all six replicates, lasting 10 min each (mean total number of food items \pm SD consumed by scaled carp 24.8 ± 1.2 and mirror carp 33.1 ± 1.4 , respectively, lin-

ear mixed model, d.f.numerator = 1, d.f.denominator = 104.9, $F = 9.13$, $P = 0.003$), and they took significantly less time to ingest the first food item [mean time (s) to ingest the first food item \pm SD of scaled carp 22.5 ± 7.0 s and mirror carp 7.2 ± 3.7 s, respectively, linear mixed model, d.f.numerator = 1, d.f.denominator = 102.8, $F = 7.2$, $P = 0.009$]. These behaviours likely contributed to why mirror carp were significantly more vulnerable to passive angling tactics than scaled carp in pond and large laboratory tank trials. However, no differences in food preferences between the two genotypes were found as indicated by similar and highly significant preferences for corn kernels over pellets by both genotypes during all six replicates lasting 10 min (mean total number of corn kernels and pellets consumed \pm SD by scaled carp 19.3 ± 1.3 and 7.9 ± 0.8 , respectively, paired t -test, d.f. = 53, $t = 9.2$, $P < 0.001$, $d > 0.8$; mean total number of corn kernels and pellets consumed by mirror carp 22.4 ± 1.4 and 12.7 ± 1.0 , respectively, paired t -test, d.

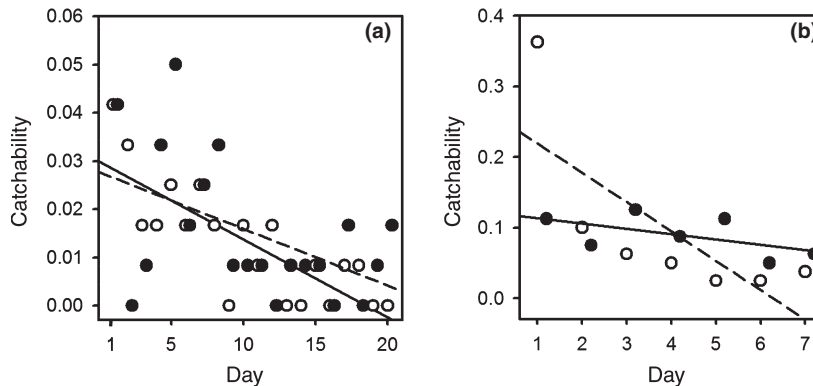


Figure 2. Daily catchability of carp (scaled and mirror carp grouped together in light of similar decline in catchability) during the day (white circles, dashed line) and at night (black circles, solid line) in relationship to the number of consecutive angling days within ponds (a) and laboratory tanks (b).

Table 2. Linear regressions to explain the time elapsed until the first angling capture of the day based on the time elapsed until the first bite of the day and the consecutive fishing day within ponds and laboratory tanks. Variance components for pond and tank replicates were very low (<1%), and therefore, analyses were conducted based on mean values of pond and tank replicates. The interaction terms were non-significant and removed from the final models

Parameter	Estimate	SE	<i>t</i>	<i>P</i>	<i>R</i> ²
Pond					
Intercept	22.634	14.89	1.52		0.80
Day of angling	3.953	1.48	2.67	0.016	
Time until first bite	0.924	0.17	5.49	<0.001	
Laboratory					
Intercept	-21.532	13.60	-1.58		0.87
Day of angling	18.928	3.17	5.98	0.004	
Time until first bite	0.380	0.65	0.59	0.590	

f. = 53, *t* = 7.3, *P* < 0.001, *d* > 0.8). These results indicate that corn kernels used as bait in the angling experiments was preferred as a food resource by both genotypes, and thus, the bait chosen in these angling experiments was not responsible for the differential vulnerability shown by scaled and mirror carp.

Discussion

Highly domesticated mirror carp were significantly more vulnerable to angling than their less domesticated scaled conspecifics in ponds, confirming the findings of previous studies (Beukema 1969; Raat 1985). In addition, the experiments showed that mirror carp were also more vulnerable to passive angling tactics within the laboratory under standardised environmental conditions, highlighting the consistency of differences in vulnerability between scaled and mirror carp. Because the two genotypes of carp used in this study were raised in a common garden, the results reveal a genetic basis of the

composite trait angling vulnerability, as previously shown for other species (Dunham *et al.* 1986; Philipp *et al.* 2009). However, daily catch rates of the two genotypes decreased over the course of the study with increasing fishing pressure, suggesting active learning effects of carp to avoid being hooked as described by Beukema (1969, 1970b) and Raat (1985). Therefore, it is expected that differential vulnerability of scaled and mirror carp to capture is most strongly expressed early in the fishing season. Additional behavioural experiments in aquaria showed that potential reasons for higher vulnerability of mirror carp compared with scaled carp could be related to higher foraging activity, faster ingestion of food items and generally higher foraging rates of the mirror carp genotype. This agrees with greater boldness of the more domesticated carp genotype (Klefoth *et al.* 2012).

With increasing angling duration, the number of captures, independent of genotype, significantly declined in both the pond and the laboratory environment. This finding is most probably related to learned hook avoidance of the fish as previously documented for carp (Beukema 1970b; Raat 1985). Because catch rates declined, but carp were observed to continue their foraging activities, learning about hook avoidance seems to have had an impact on catch rates. Learned hook avoidance usually results in reduced numbers of captures, but cues involved in learned hook avoidance behaviour of the fish can be manifold. Similar to the different cues involved in learning about natural predators, antipredator responses at increasing levels of risk (like increasing fishing pressures) include predator detection, recognition and assessment, and finally predator avoidance through flight responses (Kelley & Magurran 2003). Learning about improved responses may arise at any of these stages, but opportunities for learning are dependent on the available visual, olfactory, tactile or auditory cues

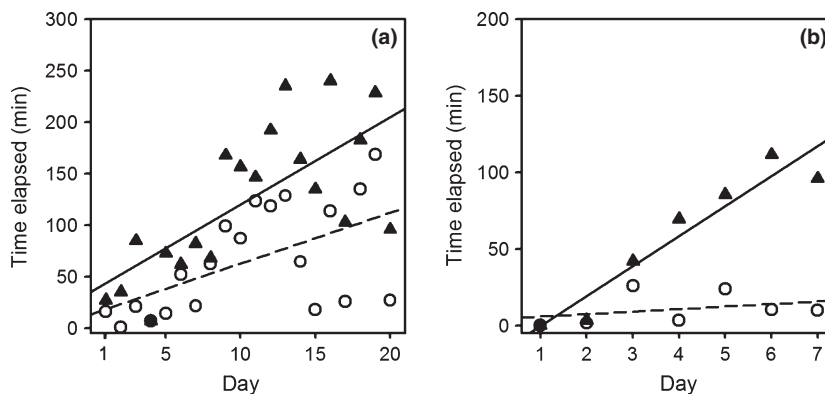


Figure 3. Time elapsed until the first bite of the fishing day (white circles, dashed line) and the time elapsed until the first capture of the day (filled triangle, solid line) in relationship to the number of consecutive angling days within ponds (a) and laboratory tanks (b).

(Kelley & Magurran 2003). Because predator detection, recognition and assessment are dependent on visual cues (Hartman & Abrahams 2000; Walling *et al.* 2004), it is conceivable that carp learned to identify the baited hook visually or learned to expel the angling bait before getting hooked. If fish learned to identify hook and line visually, catch rates should increase under environmental conditions of low visibility. Indeed, within the laboratory, carp were increasingly more vulnerable to angling during darkness with increasing fishing time and similarly, within the consistently turbid ponds, no effects of diel period on angling captures were observed. Further, if tactile cues were important in hook avoidance, fish should have ingested the angling bait, but learned to avoid getting hooked. Within the laboratory, the time until the first bite of the day remained constant over the course of the study and was not related to the time elapsed until the first capture of the day. Thus, carp ingested the angling bait, but avoided getting hooked, supporting the assumption that tactile cues were also involved in learned hook avoidance. No such effects were found within the ponds, also indicating differences in hook avoidance behaviour within different environments.

Another reason for declines in catch rates over time could be that fish reduced the number of visits to the angling locations, thereby reducing their encounter rates with the baited hook. Using a similar experimental setup, Klefoth *et al.* (2012) found that scaled and mirror carp considerably reduced their number of visits at angling locations within the laboratory, once angling started. Thus, reduced catch rates with increasing fishing duration might be related to behavioural responses of the fish towards angling-induced risk. However, within the pond environment, no such effect of angling activities on carp behaviour was observed (Klefoth *et al.* 2012); most likely because permanent latent natural predation risk induced by fish-eating birds and olfactory cues of predatory fish (despite the absence of predatory fish) was present within the pond environment, so that angling activities did not add appreciable risk-stimuli within this environment (Klefoth *et al.* 2012). Based on these findings, reduced catch rates with increasing fishing time can partly be explained by active angling location avoidance of the fish. However, the findings of Klefoth *et al.* (2012) also indicate that behavioural alterations as a response towards angling activities are dependent on the environment, and are less pronounced in more natural pond conditions. In conclusion, hook avoidance seems to be based on different responses towards angling activities including visual and/or tactile identification of the baited hook and potentially reduced visits of previously save feeding spots.

No evidence of differential learning abilities to avoid being hooked between scaled and mirror carp was found, and thus, the hypothesis was not supported. It appeared that differences in adaptation to low-risk aquaculture conditions did not impact the ability to learn to avoid hooking. This finding disagrees with studies comparing adapted learning abilities between fish originating from high- and low-risk environments (Huntingford & Wright 1989, 1992). Reasons for this opposed finding might be related to the experimental setup where groups of fish were tested together in the same ponds and laboratory tanks. Fish are generally able to make decisions about predators based on the behaviour of other fish (Pitcher *et al.* 1986) so that antipredator responses can be optimised through observations of conspecifics that have been treated by a predator (Magurran & Higham 1988; Krause 1993; Mathis *et al.* 1996). Similarly, in the present study carp of both genotypes might have learned to optimise their behaviour towards baited hooks based on observations of conspecifics. This might potentially explain rapid decreases in catch rates, but also observed approximations in vulnerability of scaled and mirror carp over the course of the fishing trials, and non-existing differences in learning abilities between scaled and mirror carp.

In the present study a certain fraction of carp was completely invulnerable to capture (45% and 15% of mirror carp and 68% and 45% of scaled carp within ponds and the laboratory, respectively) and relatively more fish of both genotypes were caught within the laboratory. In comparison, using a comparable experimental approach, Beukema (1969) found 18% of domesticated mirror carp and 33% of less domesticated scaled carp to be invulnerable to angling. These results show that environmental factors can influence the vulnerability of fish (Kuparinen *et al.* 2010), but also confirmed that individuals of the same species can differ in their intrinsic vulnerability to angling gear, as shown previously for carp and other species (Bennett 1954; Beukema 1969; Dunham *et al.* 1986; Raat 1985; Philipp *et al.* 2009). Reasons for the observed higher vulnerability of all carp within the laboratory environment were most probably related to the lack of alternative natural foraging opportunities (Klefoth *et al.* 2012). Thus, carp within the laboratory were forced to trade-off the risk of being captured and active foraging on the angling locations. Trade-off decision making between foraging and risk-taking usually depends on the hunger state of the fish (Cerri & Fraser 1983) where starved and hungry individuals tend to take higher risks than less hungry conspecifics (Godin & Crossman 1994; Damsgård & Dill 1998). The lack of natural food in the laboratory might have forced the fish to visit feeding locations despite being risky, leading to higher catch rates within the laboratory.

Potential explanations for higher vulnerability of mirror carp compared with scaled carp were derived from additional behavioural experiments under laboratory conditions. When observed solitary in aquaria, mirror carp showed higher swimming activities, ingested more food items and took significantly less time to ingest the first food item than their scaled conspecifics. All of these behavioural differences between the two genotypes very likely contributed to observed differences in vulnerability. For example, high activity during foraging likely increases the probability of encountering the baited hook, comparable to higher food encounter rates of more active swimming fish under natural conditions (Boisclair 1992). Similarly, ingesting more food increases the chances that a baited hook is ingested and a mistake is made during the sorting process and testing of ingested baits (a behaviour expressed by the carp after some exposure to angling, see Appendix S1). Increased foraging activity and higher numbers of visits at feeding locations of mirror carp compared with scaled carp have been documented for the same fish used in the present study also in the large laboratory tanks and ponds (Klefoth *et al.* 2012). In the study of Klefoth *et al.* (2012), mirror carp behaved consistently bolder than scaled carp in ponds, independent of angling activities and also mirror carp in the laboratory were found to forage more intensively at the angling locations, once fishing started. Although no differences in the number of visits at the feeding locations were observed in the laboratory before angling started, under the risk of being captured, mirror carp showed consistently higher foraging activities (Klefoth *et al.* 2012). Such behaviour can be interpreted as higher boldness level (i.e. feeding in the presence of predation risk) by the more domesticated mirror carp, which together with greater consumption of food is the most likely explanation for the greater vulnerability to capture by mirror carp relative to scaled carp. Indeed, in carp risk-taking behaviour, competitive ability, and metabolic rate are positively correlated (Huntingford *et al.* 2010). Because risk-taking behaviour, swimming activity and metabolic rate usually increase during the domestication process as a consequence of artificial selection for traits like high growth rates (Price 1999; Martin-Smith & Armstrong 2002; Biro & Post 2008; Huntingford *et al.* 2010), elevated food consumption rate and speed (this study) and generally bolder foraging behaviour (Klefoth *et al.* 2012) might have cumulatively increased the likelihood of catching mirror carp compared with scaled carp.

While boldness behaviour most likely explains higher vulnerability to angling of mirror carp, selective food preferences can be excluded as a reason for the observed patterns. Corn kernels were used as bait during angling

experiments, and scaled and mirror carp equally preferred corn kernels over pellets. Carp are known for their selective feeding and taste preferences (e.g. Jönsson 1967; Appelbaum 1980; Kasumyan & Morsy 1996), and domesticated mirror carp are known to prefer artificial pellets over natural food resources (Suzuki *et al.* 1978). However, in the present data the artificial bait corn kernel was preferred by both genotypes. Although no directed attractiveness has been associated with corn kernels when used without additional treatment (Jönsson 1967), common carp quickly locate and forage on artificial and novel food resources like corn kernels in natural environments, likely because it is more easily ingested than natural food (Bajer *et al.* 2010). The observed preferences for corn kernels in the present study could thus be based on taste preferences or other properties of the two types of food like hardness. Although carp are able to ingest, chew and digest hard particles like mussels and snails (Sibbing 1988), or angling baits such as boilies (Niesar *et al.* 2004), preferences for soft food items were reported repeatedly (Jönsson 1967; Stein *et al.* 1975; Sibbing 1988). Thus, preferences for corn kernels over pellets might be best explained by particle hardness, rather than taste preferences. Overall, however, bait preferences could be excluded as an explanation for the differential vulnerability to angling by the two genotypes of carp.

In conclusion, the present study confirmed previous findings of higher angling vulnerability of mirror carp compared to scaled carp, but differed from earlier work in terms of producing common garden reared fish from a common breeding stock. Therefore, the present study provided conclusive evidence for a genetic basis of angling vulnerability in carp, complementing work conducted in other fish species (Dunham *et al.* 1986; Philipp *et al.* 2009). Consequently, it can be predicted that anglers would remove mirror carp-like genotypes (i.e. individuals expressing high level of boldness and food consumption) from a natural population of fish when harvesting occurs at a high rate leaving behind scaled carp-types, which are more tame individuals. Alternatively, the quick learning of carp to avoid future capture introduces a new form of common pool-resource problem in fisheries that targets trophy carp based on a catch-and-release context (Arlinghaus 2007) as there should be a race for first capture among anglers to take advantage of initial high vulnerability. Finally, the present study shows that boldness represents a key phenotypic axis affecting the vulnerability of fish. This contradicts literature reporting more shy individuals to be more readily captured in other species (Wilson *et al.* 2011). Differences among these studies might be related to species-specific patterns or methodological aspects of

study designs. Future studies should try to identify the phenotypic correlates of angling vulnerability on the individual level in a variety of species to specify phenotypic traits on which angling-induced selection is acting (Uusi-Heikkilä *et al.* 2008). This work is then the basis to understand the direction of change to be expected from fisheries-induced selection (Jørgensen *et al.* 2007).

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