

Differences in predator-avoidance behavior between two invasive gobies and their native competitors

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Abstract

Globally, fish are frequently introduced beyond their native range. Some, like Ponto-Caspian gobies, are becoming invasive, achieving high colonization rates and constituting frequent prey for native predators. However, little is known about the effectiveness of antipredator behaviors of the invaders, which may shape their role in the invaded community and contribute to the invasion success. We compared antipredator behaviors of invasive gobies and native fish species after their detection by the predator, when the danger becomes direct. We studied 2 fish pairs, each consisting of an invasive and native species co-occurring in the environment and belonging to the same prey guild: (1) the racer goby *Babka gymnotrachelus* versus European bullhead *Cottus gobio*, (2) the monkey goby *Neogobius fluviatilis* versus gudgeon *Gobio gobio*, facing a naïve predator (the Eurasian perch *Perca fluviatilis*). We analyzed behaviors of single prey individuals (escaping, staying in shelter, and activity) and single predators (activity, searching, following, capturing, and latency to prey consumption). In the predator presence, the bullhead was less active and more often managed to escape after capture than the racer goby. The gudgeon escaped before the capture more often than the monkey goby. The predator succeeded later with the bullhead compared to racer goby, whereas no differences in ingestion time occurred between the gudgeon and monkey goby. The results suggest that, in terms of hunting effort of native predators, the invasive gobies are equivalent to or more profitable prey than their native analogs, which can facilitate the integration of the gobies into local food webs.

Key words: antipredator behavior, fish behavior, invasive prey, native predator, predator–prey interactions.

Invasive species are one of the greatest threats to biodiversity and community structure (Rodríguez 2006; Hughes et al. 2020; Dueñas et al. 2021). They spread spectacularly and have a strong impact on the environment (Ricciardi 2013). One important effect here is that the invasive species create new trophic relationships, and modify existing ones in recipient ecosystems. They can affect native species directly, by predation and competition (Rodríguez 2006; Levine 2008; Błońska, Grabowska, et al. 2016; Haubrock et al. 2020), or indirectly, for example, by altering predator–prey relationships of natives and therefore modifying the structure of food webs (David et al. 2017; Haubrock et al. 2019). This includes cases where invasive species influence native predators as their new prey (Crane et al. 2016; Stellati et al. 2019). Such influence can have various forms (Venable et al. 2019), depending on how effective the new prey is in predator avoidance compared to the native prey, and how these prey species interact with each other. Invasive prey can have a detrimental effect on native prey species through apparent competition (Holt 1977) due to increased predation pressure (Noonburg and Byers 2005; Castorani and Hovel 2015). On the other hand, different trophic scenarios are possible between 2 prey species that share a common predator (Harmon and Andow 2004). Positive indirect effects of one prey (here: invasive) on

the other (native) can occur when an increase in the density of the former impairs the predator's functional response to the latter due to predator saturation or predator switching (Abrams and Matsuda 1996; Webster and Almany 2002). Finally, invasive prey could constitute an integral part of the local food web, for example, by modifying the trophic level in the way that it consists almost entirely of invasives, which makes even native predators highly dependent on those invasive prey species (Bissattini et al. 2021). There is a need for understanding how particular biological features of invasive species determine their availability as prey for native predators, and how they perform compared to native species belonging to the same prey guild, that is, in situations when their distributions overlap temporally and spatially and they share the same predators. Assessing prey antipredatory strategies in this context is important in a broader perspective for predicting the outcome of new trophic linkages created by invasive species, and their impact on food webs.

Prey exhibit predator-induced defenses involving changes in morphology (e.g., McCollum and Leimberger 1997; Boersma et al. 1998; Dahl and Peckarsky 2002), life history (Tams et al. 2018), and behavior (Lima and Dill 1990; Sparrevik and Leonardsson 1999; Johansson et al. 2004). Behavioral defenses involve spatial avoidance, increased hiding,

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decreased activity, diet change (Mikolajewski and Johansson 2004; Teplitsky and Laurila 2007), escape, deterrence, and freezing (Lima and Dill 1990). These responses are considered components of the predator-avoidance strategy in prey, representing a sequence of events taking place consecutively from the detection of the predator by the prey until it is finally consumed or successfully escapes (Kelley and Magurran 2003). Particularly noteworthy is the final period of a predator-prey interaction, when a prey individual is detected by a predator and prey responses are most intense. This is the peak active phase of predator avoidance that precedes the time when prey is eaten (ingested). The moment of ingestion is decisive and should be taken into account, as capture does not necessarily mean death. Indeed, prey can defend themselves, for example, by using spines and/or toxins (Hasegawa et al. 2021) and successfully avoid ingestion even after capture.

On the global scale, fishes are one of the taxa most commonly introduced outside their native range (Gozlan 2008; Haubrock et al. 2022). We focused on the gobies, as their invasions are considered amongst the most impressive freshwater fish invasions within Central and Western Europe (Copp et al. 2005; Roche et al. 2013). Six invasive goby species are currently present in European waters (Copp et al. 2005), including the racer goby *Babka gymnotrachelus* (Kessler 1857) and the monkey goby *Neogobius fluviatilis* (Pallas, 1814). These species have spread successfully in freshwaters, especially in the river Vistula (Płachocki et al. 2020), which is one of the largest rivers in the Baltic Sea region (HELCOM 2018). We investigated the antipredator behavior of the racer and monkey gobies by pairing them with native species from the same guild, as this may help to answer the question of whether this aspect of their biology can constitute an advantage to the invasive gobies compared to the local species threatened by their invasions. The racer goby is often found in the same locations as the European bullhead *Cottus gobio* (Linnaeus, 1758) (Janáč et al. 2018). Substantial habitat overlap between these 2 species was revealed in a lowland European river in locations with medium water velocities on stony and gravely substrate (Kakareko et al. 2016). The racer goby was able to outcompete the European bullhead for food (Kakareko et al. 2013) and shelter (Jermacz et al. 2015; Błońska, Kobak, et al. 2016; Grabowska et al. 2016) in laboratory experiments. On the other hand, the monkey goby occupies sandy bottom areas, which are also optimal for the gudgeon *Gobio gobio* (Linnaeus, 1758) (Kottelat and Freyhof 2007; Płachocki et al. 2020). Increasing monkey goby densities have been observed to coincide with declines in gudgeon populations (Jakovlić et al. 2015).

The invasive gobies are a common, often dominant dietary item of predators in invaded areas (Reyjol et al. 2010; Płachocki et al. 2012), which may suggest the lower security of the invader in the mixed-species guild. However, it is important to note that high densities and thus high availability of the gobies as prey for predators are also important. According to the theory of optimal foraging (Werner and Hall 1974; Pyke and Starr 2021), predators are expected to select the types of prey that provide the greatest net energy gain, and these are usually the most abundant and easily captured organisms available in the environment. High abundances of the gobies are recorded in colonized environments (Kakareko et al. 2009, 2016), and so they are potentially widely available prey for predators. Nevertheless, in an experimental study on behavioral reactions to predation cues (prey skin extracts), the gudgeon exhibited thigmotaxis and reduction in horizontal and vertical mobility, while the monkey goby did not

show any of those behaviors (Kłosiński et al. 2022). This suggests that weaker antipredator responses of invasive gobies may indeed contribute to their susceptibility to predation in invaded areas. In our current research, we assessed whether the behavioral responses of the gobies to direct predation danger follow the same pattern, that is, are less pronounced in invasive than native species. This, in the light of studies indicating that the invasive gobies are a common, often dominant dietary item of predators in invaded areas (Reyjol et al. 2010; Płachocki et al. 2012) may suggest the lower security of the invader in the mixed-species guild.

Our main goal was to assess the differences in antipredatory behavior and its effectiveness between 2 invasive Ponto-Caspian goby fish (Gobiidae) and their native counterparts. We focused on prey behavior in the final, the most active stage of a predator-prey interaction, that is, when a reciprocal detection by both sides (predator and prey) has occurred, until a successful ingestion of prey or avoidance of predation. We hypothesized that (1) under direct predation danger, the invasive gobies would present qualitatively different behavior than their native counterparts, displaying different sets of species- or family-specific traits. This is because the invasives, although their habitat requirements are similar to those exhibited by their native counterparts, belong to a taxonomically different, specific family of fish: freshwater Gobiidae (in our research, natives were from Cottidae and Cyprinidae families) that are among the most invasive species in Europe (Copp et al. 2005). (2) Antipredator behavior of the invasive gobies would be less pronounced and effective, that is, would make them easier to be caught and ingested by the predator compared to the native prey species. This is based on the assumption that the invaders in a novel range can benefit from the allocation of more energy resources to growth and reproduction at the cost of weaker antipredatory defenses, which makes them better competitors than the native species in the same area (in accordance with the Evolution of Increased Competitive Ability hypothesis, Blossey and Notzold 1995; Callaway and Ridenour 2004).

We compared results only within the above-mentioned pairs, as they were composed of species coexisting and interacting with each other in the same environments. We assumed that to become effective invaders, alien organisms need to perform better than the natives encountered in a particular co-occupied habitat, rather than generally in all communities.

Materials and Methods

The main idea of the experiment

We focused on checking if the behavioral differences between particular prey species make them more or less difficult to capture and, most importantly, successfully ingest during a direct predator encounter, that is, in the phase when the prey has been detected and exposed to the predator attack. Therefore, the approach enabling the physical contact of the prey with the predator was crucial for answering the questions we posed. We focused on particular prey characteristics which make them easier or more difficult to catch (i.e., behavior). As this is difficult to observe in a natural, heterogeneous environment, we needed to use laboratory experiments to separate the features of interest from the influence of environmental conditions (bottom substrate, macrophytes, water flow, etc.). Thus, we designed an experimental setup to enable the predator to hunt directly on the prey of a given species in an identical, standardized environment to check the influence of species-specific traits (mobility, morphology) in defense

against predator attacks. The prey had the opportunity to hide inside a shelter (mesh area accessible to prey but not to the predator) or swim freely outside, facing the predator (Figure 1). To make sure that both prey species in each pair will have the same opportunities and conditions at the start of the experiment, we chose naïve, laboratory-reared specimens of the Eurasian perch *Perca fluviatilis* (Linnaeus, 1758) as predators. The perch is often found in habitats occupied by all the tested prey species (invasive and native) (Nesbø et al. 1999) and foraging on them (Płachocki et al. 2012; Kakareko et al. 2016). As the Ponto-Caspian gobies are mostly eaten by medium-sized predators (Reyjol et al. 2010; Płachocki et al. 2012), the perch represents an optimal model species to study predator effects on the invasive gobiids and co-occurring native fish species. The use of naïve perch allowed us to eliminate the potential perch preference for one of the studied species resulting from its experience acquired in the natural environment. As we had a limited number of perch individuals, we decided to expose both prey species in the pair to the same perch individual (i.e., each perch individual had the opportunity to interact with both prey species within a given pair, one after the other). However, it must be acknowledged that the predator might gain some experience after consuming the first prey individual. To control for this, we applied a 2 × 2 cross-over design, with various predator individuals offered either a goby or a native species as the first prey.

Animals

We collected the prey fish from the wild in July 2019 and kept them in stock tanks for at least 1 month before the start of experiments. European bullhead and racer goby were collected from the river Brda in central Poland (53°08′52.5″N 17°58′10.5″E) by a diver using an aquarium net. Gudgeon and monkey goby were collected using electrofishing (EFGI 650, Bretschneider Spezial Elektronik, Germany) from the river Pilica in east central Poland (51°45′50.1″N 21°08′55.5″E). We used different fishing methods due to the characteristics of the species and environments. The European bullhead and racer goby in the river Brda were mainly located in shelters (under rocks, roots, etc.) that were easier to be accessed by a diver than by electrofishing. The gudgeon and monkey goby

were located on the open bottom, where the electrofishing method was effective. The differences in methods did not disturb the results, as fish were compared in pairs collected from the same environment, using the same method. All the fish were of 0+ age, without any external signs of sexual maturity and thus we did not determine their sex.

After capture, we transported the fish in plastic bags containing water and oxygen to the air-conditioned laboratory and held them in 350-L stock tanks (20–30 individuals per tank) filled with conditioned tap water (temperature maintained by air conditioning at 16.1 ± 0.5 °C, pH 8.15 ± 0.15 , electrical conductivity 608.4 ± 4.5 µS/cm, oxygen level 8.13 ± 0.25 mg/L and $82.5 \pm 3.06\%$; measured with Multi 340i Meter, WTW, Weilheim, Germany) and equipped with standard aquarium filters and aerators. The photoperiod was set at a 14:10 h light:dark cycle with lights on at 0700 h. The stock tanks were equipped with ceramic and stony shelters and had no bottom substrate. We fed the fish daily ad libitum with frozen chironomid larvae and exchanged water in the tanks once a week (ca. 30% of the water volume) to ensure appropriate level of animal welfare.

Naïve Eurasian perch *P. fluviatilis* was bred from larvae obtained during controlled reproduction of wild breeders captured during commercial catches in early April in accordance with the previously established procedure (Żarski et al. 2011). Fertilized eggs were incubated in a flow-through recirculating system. Larvae hatched on day 8th post-fertilization and were reared at 14 °C, photoperiod 16:8 h light:dark, and oxygen concentration of 8.5 mg/L. Larvae were fed ad libitum with mixed *Artemia* sp. nauplii (INVE, Belgium) and a commercial formulated diet (Perla Larva Proactive 5.0, TrouvitNutreco, The Netherlands) 6 times a day. After 30 days of rearing, juveniles of perch were fed with a commercial diet (Perla Larva Proactive 4.0) and frozen Chironomidae larvae. At the age of about 2 years, the perch (40 specimens) was transported from the breeding facility to the air-conditioned laboratory and kept in an 800-L stock tank filled with conditioned tap water. For 3 months before the start of the experiments, the perch was kept in our laboratory in the same light and temperature conditions as the prey species.

The fish were weighed in a bucket with water before the start of the experiment, and their total body length was measured with ImageJ 1.49v program (freeware by W.S. Rasband, U.S. National Institutes of Health, Bethesda, MD, USA) using digital images taken from the recorded videos.

Although in our research we exposed the tested prey individuals to direct physical contact with a predator, this was the only way to obtain answers to the questions raised. Nevertheless, we did our best to adhere to the ASAB/ABS (2019) guidelines for the use of animals in research by providing them with appropriate housing conditions and obtaining permission from the Local Committee for Ethics in Animal Research in Bydgoszcz, Poland (statement no. 50/2017 from 28 September 2017). The housing conditions guaranteed animal welfare, which was manifested by the overall activity and food intake of the fish throughout the research period. We did not notice any external signs of stress or disease (e.g., unnatural body shape, skin changes, swimming problems). After the experiments, the European bullhead and gudgeon that remained uneaten or were not used in the experiments were released where they were caught. Other fish (invasive gobies and Eurasian perch) were euthanized by an overdose of Tricaine Methanesulfonate (MS-222) and disposed of.

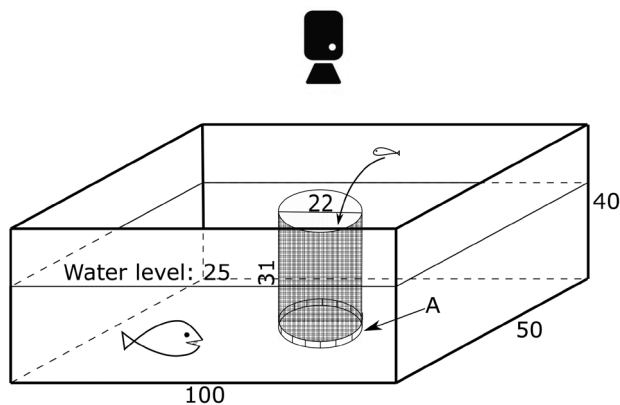


Figure 1. Experimental setup. The predator (perch) was placed in an experimental tank alone to acclimatize. A single prey individual was placed always inside a mesh cylinder acting as a hideout for prey (A). During a single trial, a perch individual was confronted with both prey species from the pair (one after another) in a sequence varying among replicates (native before invasive or invasive before native). Dimensions are given in centimeters.

Experimental setup

Experiments were conducted in a 200-L tank (100 cm × 50 cm × 40 cm, length × width × height) filled with conditioned tap water and isolated from external stimuli with Styrofoam screens. In the center of the tank, we placed a cylinder (height: 31 cm, diameter: 22 cm) made from a wireframe and plastic mesh (1 mm in diameter) (Figure 1). There was a 1.5-cm gap between the tank bottom and the lower edge of the mesh (marked as A in Figure 1). Thus, prey fish could use it as a shelter, while a predator was too large to get inside. Above the tank, we placed an IP video camera (Samsung SNB-6004P, Changwon, South Korea), which could catch the view of the entire experimental tank. Before the experiments, the tank was equipped with a filter and air stone to maintain appropriate water quality. The filter and air stone were pulled out after a prey fish was placed in the experimental tank to prevent water surface movement, which could disturb the video analysis. The photoperiod and water temperature in the experimental tank were the same as in the stock tanks (14:10 h light:dark cycle, c.a. 16 °C).

Experimental procedure

During each trial, a single predator (perch specimen) was confronted with a single prey individual in 2 successive rounds, so that each predator interacted with both prey species from the pair, one after another. The experiment started by placing a single predator in the experimental tank at 2100 h (Figure 2). After 12 h, we fed it ad libitum with Chironomidae larvae to standardize its hunger level. The experiment was continued only when the predator consumed food, indicating its acclimation to the experimental setup. Twenty-four hours after predator feeding (i.e., at 0900 h), we removed the filter and air stone and placed the first prey specimen from a particular pair of prey species in the experimental tank inside the shelter (mesh cylinder) (first round). Then, the predator had 8 h to consume (i.e., swallow) the prey. The timing of prey ingestion was recognizable based on the movements of the perch's operculum. The capture of the prey was followed by intense movements of the gill lids. The cessation of these movements was considered as the swallowing of the prey, because it never happened that the prey was released from the mouth of the predator after this event. If the prey individual was not consumed, we removed it from the experimental tank. Whether or not the prey was eaten, 24 h after the first prey specimen was placed in the experimental tank, we fed the predator again with Chironomidae larvae ad libitum. The filter and air stone were placed back into the tank. After the following 24 h, we removed the filter and air stone again and placed the second prey specimen (at 0900 h), belonging to the other prey species of the given pair (second round). For each trial, we selected prey individuals of similar sizes (in total length) in each pair. The predator had another 8 h to consume the prey and that was the end of a single trial (Figure 2). We exchanged about 25–30% of water volume between trials. The interval between trials was 28 h. Within each prey species pair, the predators were divided into 2 groups, one facing first the invasive prey and then the native one, and the other confronted consecutively with the native prey and then the invasive one. Each predator individual was used in only 1 trial with 2 rounds (prey individuals).

Each prey species pair was studied separately. In total, we included 11 trials for the European bullhead (mean ± SD: individual weight = 0.53 ± 0.16 g; length = 4.51 ± 0.57 cm)/

racer goby (0.50 ± 0.28 g; 4.39 ± 1.07 cm) and 15 trials for the gudgeon (0.87 ± 0.28 g; 5.86 ± 1.07 cm)/monkey goby (0.88 ± 0.30 g; 5.36 ± 1.18 cm) pairs in the analysis. There were no differences in weight (paired *t*-test for the European bullhead/racer goby: $t_{10} = -0.70$, $P = 0.494$; for the gudgeon/monkey goby: $t_{13} = -0.26$, $P = 0.801$) and length ($t_9 = 0.40$, $P = 0.703$ and $t_9 = 1.16$, $P = 0.279$, respectively) between prey individuals in each pair. The weight and length of the perch specimens used for the European bullhead/racer goby pair were 43.6 ± 17.4 g and 19.86 ± 3.34 cm, whereas the weight and length of the perch exposed to the gudgeon/monkey goby pair were 46.1 ± 17.2 g and 21.73 ± 2.76 cm, respectively. There were no differences in perch weight and length between the 2 prey pairs (*t*-test: $t_{22} = 0.34$, $P = 0.735$ and $t_{18} = -1.36$, $P = 0.189$, respectively).

Video analysis

Each round of the trial lasted 8 h or until the prey was consumed by the predator. The videos were analyzed semi-automatically using the BORIS 7.9.7 software (Friard and Gamba 2016; Behavioral Observation Research Interactive Software, freeware, www.boris.unibo.it). We noted several continuous events (long-term episodes, for which the duration was determined and expressed as % of the total experiment time, i.e., 8 h or till the prey ingestion, if not stated otherwise below) and point events (short-term incidents, for which the number of occurrences were determined) concerning prey and predator behaviors, based on Savino and Stein (1989) and Beauchamp et al. (2007). All noted variables are included in Table 1.

All the videos were analyzed by the same person to avoid any differences due to the subjective assessment by the observer.

Statistical analysis

We performed a Principal Component Analysis (PCA) on the correlation matrix, separately for prey and predator behaviors in each prey pair, to reduce the number of behavioral variables and detect possible relationships between them. The principal components were extracted based on their eigenvalues greater than 1. When explaining the meaning of the obtained principal components, we took into account the original variables with absolute values of their loadings higher than 0.5 after Kaiser-Varimax rotation. The principal components determined by the PCA were analyzed using a 2-way mixed analysis of variance (ANOVA) for cross-over designs (separate for

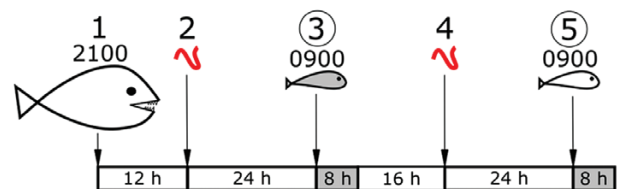


Figure 2. Experimental procedure. 1—releasing the predator (perch) to the tank; 2—the first feeding of the predator with Chironomidae larvae ad libitum; 3—placing the first prey individual in the tank; 4—the second feeding of the predator with Chironomidae larvae ad libitum; 5—placing the second prey individual (of different species than in step 3) in the tank. White rectangles indicate predator acclimation periods. Numbers in circles and gray rectangles indicate the recorded and analyzed periods (rounds) of the trial.

Table 1. The list of variables noted during the video analyses

Prey		Predator	
Behavior	Description	Behavior	Description
Continuous events			
Inactivity	The prey individual not swimming in any part of the tank	Inactivity	The predator not swimming
Exploration	The prey individual actively exploring the tank, undisturbed by the predator	Search	The predator swimming with no obvious signs of interest in the prey individual
Staying in shelter	The prey individual staying inside the cylinder, inaccessible to the predator	Latency to consume the prey	The time from the prey introduction to its successful consumption by the predator (continuous, measured in s) – the prey that survived the experiment was assigned the maximum value of 8 h (28 800 s)
Point events			
Escape	The prey individual rapidly moving away from the predator present in a close distance	Following	The predator maneuvering toward the prey individual to maintain a close distance and seek an opportunity to attack
		Strike	The predator attempting to grasp, injure, or stun prey
		Capture	The predator catching the prey, prey disappearing in the predator's mouth

each prey species pair). Factors in the ANOVA were set as (1) round of the experiment (the first and second prey individuals of 2 different species, offered consecutively to the predator) as a within-subject factor, (2) sequence (the sequence of offering the prey species to the predator: invasive after native or native after invasive) as a between-subject factor. The effect of prey species was coded in this design indirectly as a round × sequence interaction, whereas the factor sequence indicated potential carryover effects (Díaz-Urriarte 2002; Jones and Kenward 2003). The data were mostly normally distributed (Shapiro–Wilk test) and variances were homogenous (Levene test). All analyses were performed using IBM SPSS Statistics 26.0 (IBM Corp.).

Results

The original behavioral variables included in the analysis are presented in [Supplementary Materials A and B](#). The PCA ([Table 2](#)) extracted 2 principal components for prey behavior and 3 principal components for predator behavior in the European bullhead versus racer goby pair, as well as 2 principal components for prey behavior and 2 principal components for predator behavior in the gudgeon versus monkey goby pair.

European bullhead versus racer goby

All individuals of the European bullhead and racer goby were ingested by the predator. The principal component meanings were assigned as follows: (1) prey behaviors: Activity (PC1), Escape (PC2); (2) predator behaviors: Activity (PC1), Efficiency of attacks (PC2), Delay in success (PC3). The prey species differed from each other (as indicated by a significant round × sequence interaction) in the activity ([Table 3A](#)): European bullhead was less active than racer goby ([Figure 3A](#)). Both prey species showed similar escape responses ([Table 3B](#); [Figure 3B](#)). There was a significant effect of the round on predator activity ([Table 3C](#)): The perch were less active during round 2 (data not shown) regardless of the prey sequence. The efficiency of perch attacks was similar when facing both prey species ([Table 3D](#); [Figure 3D](#)). However, the predator succeeded later when foraging on the European bullhead than on the racer goby ([Table 3E](#); [Figure 3E](#)).

Gudgeon versus monkey goby

There were 3 gudgeon and 5 monkey goby individuals which survived the experiment. The following meanings were attributed to the principal components: (1) prey behaviors: Activity (PC1), Escape (PC2); (2) predator behaviors: Predation intensity (PC1), Activity (PC2). There were no differences between the prey species in activity ([Table 4A](#); [Figure 4A](#)). However, the prey species differed from each other (as indicated by a significant round × sequence interaction) in their escape behavior ([Table 4B](#); [Figure 4B](#)): Gudgeon initiated escape behavior more often than monkey goby ([Figure 4D](#)). Additionally, visual inspection of the video recordings revealed that the gudgeon exhibited more sophisticated escape events, performing series of escapes (multiple movements) rather than single point escapes shown by its invasive counterpart. Moreover, prey escape behavior depended significantly on the main effect of round: Both species escaped more often in the second round of the experiment, regardless of the prey sequence (data not shown). The predator behavior was not affected by round, sequence, and prey species ([Table 4C, D](#); [Figure 4C, D](#)).

Table 2. Results of the principal component analyses on predator and prey behavioral variables

	PC ^a	λ^b	% Variance ^c	Variable loadings ^d
European bullhead vs. racer goby				
Prey behavior				
PC1 Activity		2.3	57.2	Inactivity (-0.949), Staying in shelter (-0.661), Exploration (0.954)
PC2 Escape		1.1	25.8	Escape (0.934)
Predator behavior				
PC1 Activity		2.1	35.7	Search (0.992), Inactivity (-0.990)
PC2 Efficiency of attacks		1.4	24.7	Strike (-0.937), Capture (-0.710)
PC3 Delay in success		1.3	19.6	Latency to consume the prey (0.719), Capture (0.582), Following (-0.635)
Gudgeon vs. monkey goby				
Prey behavior				
PC1 Activity		2.0	50.5	Exploration (0.993), Inactivity (-0.991)
PC2 Escape		1.0	21.1	Escape (0.908)
Predator behavior				
PC1 Predation intensity		2.5	41.3	Latency to consume the prey (-0.768), Strike (0.805), Following (0.672), Capture (0.780)
PC2 Activity		1.9	31.9	Inactivity (-0.989), Search (0.983)

^aPrincipal components discriminated by the PCA.

^bEigenvalue of the principal component.

^cPercentage of variance explained by the principal component.

^dCorrelations of measured variables with the principal component (loadings with absolute values higher than 0.5 are shown).

Discussion

We studied the behavior of individual fish exposed to imminent danger from a predator - a naïve Eurasian perch specimen. The prey were invasive Ponto-Caspian gobies and their native counterparts, compared in 2 pairs of species (invasive vs. native) co-occurring in the environment: the racer goby versus European bullhead, the monkey goby versus gudgeon. Our main aim was to determine the differences in antipredator behavior and its effectiveness between the invasive goby fish and their local native analogs. We confirmed our first hypothesis showing that invasive gobies, when facing a direct predator danger, present different behaviors than their native counterparts. However, our second hypothesis was only partially confirmed: In one of the prey species pairs, the native European bullhead turned out to be more difficult for the predator to hunt. On the other hand, in the other species pair, predator efficiency was similar in the presence of both prey species, despite differences in their behavior.

In the first pair of prey species tested, the European bullhead was less active and spent more time in the shelter. The shelter plays a significant role in the biology of both prey species as they spent there most of their time during the day (Mills and Mann 1983; Grabowska et al. 2016, 2019). However, here we have found for the first time that the racer goby used the hideout to a lesser extent than the bullhead facing the direct threat from a predator. The Eurasian perch is a visually oriented predator (Diehl 1988) and more mobile gobies

were more visible, thus increasing their risk of being eaten under daylight and clear water conditions in our experiments. Thus, the longer exploration time exhibited by the racer goby suggests that, despite a direct predator danger, the invasive species take more risk and explores the environment. On the other hand, individuals showing greater exploratory activity can more efficiently compete for environmental resources and benefit from improved feeding opportunities, thus showing increased growth and/or fecundity (Huntingford et al. 1990; Fraser et al. 2001). These considerations involve differences on an interspecific level; however, individuals from the same species may also display different personalities, that is, individual differences in boldness, exploration, aggressiveness, etc. (Sih et al. 2004; Kaiser and Müller 2021). Such intraspecific variation can strongly influence a biological invasion (Juette et al. 2014). For example, the presence of bold individuals may help invasive populations to spread further (Chapple et al. 2012). It is possible that, due to its invasive character, the population of the racer goby studied in our experiment contains a higher frequency of bold individuals than that of the European bullhead, which can explain the observed differences. Nevertheless, confirmation of this possibility requires further investigation.

In the second pair of coexisting prey species, the gudgeon exhibited more sophisticated escape events following predator attacks than the monkey goby, performing a series of multiple escapes rather than single movements exhibited by its invasive counterpart. Different escaping strategies may be

Table 3. Two-way ANOVA for cross-over designs to test the behaviors of the European bullhead and racer goby (A, B) as well as their predator (perch) (C–E)

Principal component	Effect	df	MS	F	P
(A) Prey PC1, Activity	Round (R)	1	0.76	1.63	0.233
	Prey species (R × S)	1	10.12	21.64	<0.001*
	Error	9	0.47		
	Sequence (S)	1	1.29	2.16	0.175
	Error	9	0.60		
(B) Prey PC2, Escape	Round (R)	1	0.37	0.45	0.519
	Prey species (R × S)	1	0.04	0.05	0.827
	Error	9	1.09		
	Sequence (S)	1	0.35	0.41	0.540
	Error	9	0.85		
(C) Predator PC1, Activity	Round (R)	1	2.77	7.45	0.023*
	Prey species (R × S)	1	<0.01	<0.01	0.991
	Error	9	0.37		
	Sequence (S)	1	1.43	0.97	0.350
	Error	9	1.47		
(D) Predator PC2, Efficiency of attacks	Round (R)	1	2.29	2.10	0.181
	Prey species (R × S)	1	1.71	1.57	0.243
	Error	9	1.09		
	Sequence (S)	1	0.35	0.41	0.540
	Error	9	0.85		
(E) Predator PC3, Delay in success	Round (R)	1	1.37	4.75	0.057
	Prey species (R × S)	1	3.52	12.16	0.007*
	Error	9	0.29		
	Sequence (S)	1	0.26	0.20	0.666
	Error	9	1.28		

The round of the experiment (the first and second prey individuals of 2 different species offered consecutively to the predator) was set as a within-subject factor, sequence (the sequence of offering the prey species to the predator: invasive after native, or native after invasive, indicating potential carryover effects) as a between-subject factor. The effect of prey species was coded as a round × sequence interaction. Asterisks indicate significant effects at $P < 0.05$.

associated with differences in anatomy and lifestyle characteristics of the prey species, which translate into their swimming abilities. Although the species we selected for both pairs are similar in terms of habitat requirements, body size and shape, they do show anatomical differences affecting their locomotor abilities. The gudgeon has a swim bladder, which makes its lifestyle more benthopelagic (Egger et al. 2021). On the contrary, a swim bladder is absent in the monkey goby (Neilson and Stepien 2011; Teletchea and Beisel 2018) and its pelvic fins form a suction organ increasing its ability to attach to the bottom (Kottelat and Freyhof 2007), which makes it more dependent on the bottom substrate. Thus, gobies are considered poor swimmers (Teletchea and Beisel 2018). Egger et al. (2021) showed that the gudgeon had better swimming performance compared to another Ponto-Caspian gobiid, the round goby *Neogobius melanostomus* (Pallas, 1814). The authors pointed out that because of the characteristic body shape, which is not adapted to prolonged swimming, benthic fish, such as gobies, display a burst-and-hold swimming mode. In conjunction with the results of Kłosiński et al. (2022), showing the thigmotaxis and dispersion of the gudgeon in response to the alarm substance, this increased number of escapes suggests avoidance of the dangerous area as the main antipredator behavior of this species. Instead, the monkey goby seems to rely on activity reduction

allowing it to avoid detection by predators (Čápková et al. 2008; Jakubčínová et al. 2017).

The European bullhead turned out to be more difficult for the predator to hunt than the racer goby, while in the second prey pair predator efficiency was similar in the presence of the gudgeon and the monkey goby. The perch captured the European bullhead more often and needed more time for the final successful ingestion of the bullhead, although spent less time following the bullhead than the racer goby. The higher number of captures of the European bullhead means that this prey species was able to get released from the predator’s mouth more often than the racer goby. The bullhead has morphological structures missing in the racer goby, which can be considered as antipredator adaptations reducing capture success: a strong rear-pointing spine protruding from the operculum (Witkowski and Terlecki 2000; Tomlinson and Perrow 2003) and tiny spines on the body, especially near the pectoral fins (Witkowski and Terlecki 2000). The shorter following time may be due to the lower activity of the European bullhead, giving the perch fewer opportunities to actively follow this prey species. All in all, the perch succeeded later when facing the native European bullhead than the invasive racer goby. The strategy that enables the European bullhead to escape from the predator’s mouth after capture may be effective in natural, large-scale environments,

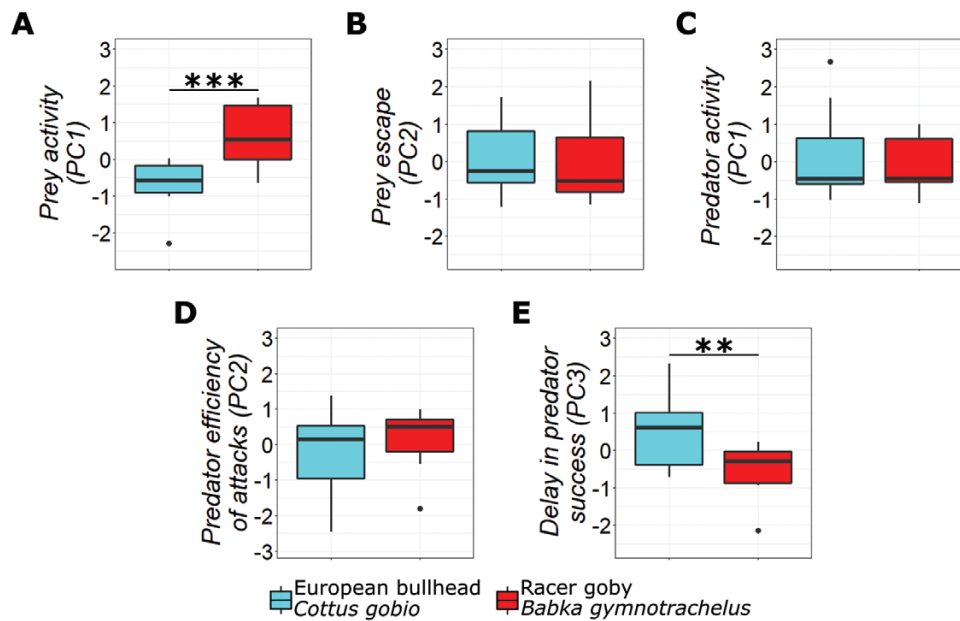


Figure 3. Behaviors of the European bullhead (blue/light) and racer goby (red/dark) (A, B) as well as of their predator (perch) (C–E). A—prey activity; B—prey escape; C—predator activity; D—predator efficiency of attacks; E—delay in predator success. Asterisks indicate significant differences: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (see online for color figures).

Table 4. Two-way ANOVA for cross-over designs to test the behaviors of the gudgeon and monkey goby (A, B), as well as their predator (perch) (C–D)

Principal component	Effect	df	MS	F	P
(A) Prey PC1, Activity	Round (R)	1	0.27	0.25	0.627
	Prey species (R × S)	1	0.02	0.02	0.894
	Error	13	1.08		
	Sequence (S)	1	0.59	0.54	0.474
	Error	13	1.09		
(B) Prey PC2, Escape	Round (R)	1	4.39	6.21	0.027*
	Prey species (R × S)	1	3.67	5.19	0.040*
	Error	13	0.71		
	Sequence (S)	1	2.00	2.83	0.117
	Error	13	0.71		
(C) Predator PC1, Predation intensity	Round (R)	1	<0.01	<0.01	0.998
	Prey species (R × S)	1	0.68	1.28	0.279
	Error	13	0.53		
	Sequence (S)	1	1.21	0.78	0.393
	Error	13	1.68		
(D) Predator PC2, Activity	Round (R)	1	0.18	0.35	0.564
	Prey species (R × S)	1	0.12	0.24	0.631
	Error	13	0.50		
	Sequence (S)	1	0.56	0.34	0.572
	Error	13	1.55		

The round of the experiment (the first and second prey individuals of 2 different species, offered consecutively to the predator) was set as a within-subject factor, sequence (the sequence of offering the prey species to the predator: invasive after native, or native after invasive, indicating potential carryover effects) as a between-subject factor. The effect of prey species was coded as a round × sequence interaction. Asterisks indicate significant effects at $P < 0.05$.

because the predator, discouraged by a failed attack, may lose interest in that particular prey individual. A disincentive here, according to the optimal foraging theory (Pyke and Starr 2021), would be the higher energy costs incurred by the predator due to extended handling time. However, we must be aware that any capture is usually associated with harm to

the prey's body. The ability of the bullhead to actively escape from the predator's mouth allows it to survive a direct predator attack, but it is difficult to predict the long-term survival costs of such an escape and this may require further research. We observed that the European bullhead was the only prey studied which exhibited a zig-zagging escape trajectory

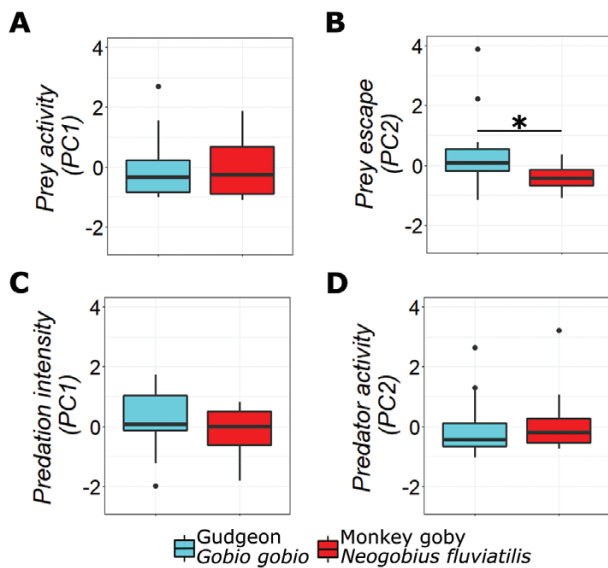


Figure 4. Behaviors of the gudgeon (blue/light) and monkey goby (red/dark) (A, B), as well as of their predator (perch) (C, D). A—prey activity; B—prey escape; C—predation intensity; D—predator activity. Asterisks indicate significant differences: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (see online for color figures).

(personal qualitative observations, not analyzed formally) which is considered an escape behavior with multiple direction changes increasing the chances of survival (Ros et al. 2019). This may also increase the survival of the European bullhead in the wild by confusing the predator, which may lose interest and switch to another prey individual. Our findings suggest that the racer goby, being easier to catch and swallow for the Eurasian perch than the European bullhead, is more beneficial for predators in terms of hunting effort than the native prey from the same guild. On the other hand, the monkey goby, being similarly susceptible to capture and ingestion by Eurasian perch as the gudgeon, is equivalent to its native analog from the same guild as prey for local predators, in terms of the hunting effort of predators.

It should be noted that in our study, antipredatory responses of the gudgeon, although more sophisticated, were not more effective than those of its invasive goby counterpart. Moreover, the European bullhead was finally hunted successfully by the predator, even though it took more time than in the case of the invasive goby. However, we must be aware that our study was geared specifically toward the behavior of prey facing direct threat from a predator, that is, in the phase when the prey has been detected and is exposed to the predator attack. Laboratory experiments were the only possible way to observe the locomotion of fish in repeatable conditions. The strategies of the natives, compared to the invasive gobies, involved a greater number of more varied movements and therefore might be more effective on a wider spatial scale. It is known that the spatial structure of the environment may affect the predator–prey relationships (Mercado-Vásquez and Boyer 2018), because an animal in a confined space cannot perform a straight long-distance relocation, moving away from a dangerous location (Cuddington and Yodzis 2002). In an environment where the space is not limited, the European bullhead may discourage the predator by escaping from its mouth and confuse it by zig-zagging, thus gaining an advantage over the racer goby, whereas the

gudgeon would be likely to gain an advantage over monkey goby by moving away from the predator to a safe distance. Nevertheless, laboratory experiments can provide valuable data on interspecific differences in prey behavior, when their results are interpreted taking the above-mentioned limitations into account. The above considerations provide a rationale for believing that under natural conditions, the higher profitability of the invasive gobies as prey for local predators over their native counterparts can be even greater than our laboratory study suggests.

Finally, our results support the idea that the 2 invasive gobies are potentially attractive prey for predators in their novel environments, as we found no greater defensive capacity in these fish compared to the native species. However, extrapolation of these conclusions to other Ponto-Caspian gobies must be done with care. A similar experimental study conducted on the invasive Ponto-Caspian round goby *N. melanostomus* showed that the native predators, the burbot (*Lota lota*) and smallmouth bass *Micropterus dolomieu*, hunted the round goby less efficiently than a native cottid prey species, the mottled sculpin *Cottus bairdii* (Michels et al. 2021). One of the reasons for the discrepancy between the studies may be morphological differences between the gobiids (Jakubčínová et al. 2017). The round goby is discriminated from the other goby species by a significantly deeper caudal peduncle, which may be associated with their better locomotion abilities (Jakubčínová et al. 2017) and, consequently, better ability to escape from attacks of predators. Nevertheless, the shorter, less pronounced, and less diverse defensive behavior we recorded in the invasive gobies is consistent with the study by Kłosiński et al. (2022), who showed that the monkey goby is generally less responsive to the damage-released chemical alarm cues compared to the gudgeon. Thus, our findings suggest that the significant share of the invasive gobies in the predator diet may be not only due to their high density (Płachocki et al. 2012; Crane and Einhouse 2016; Mikl et al. 2017), according to the optimal foraging theory (Werner and Hall 1974; Pyke and Starr 2021), but also because of the weak behavioral defenses of invasive gobies against predators. Additionally, if this lower defense activity is associated with a reduction in energy expenditure, it may give the gobies an advantage over native fish species in the environments where the predation risk is low, as they may allocate more energy to growth or fecundity rather than to defense against a predator. However, as the invasive gobies do not exhibit more effective defense behavior when facing direct predator danger, they might lose their advantage over native fish in high-risk areas. The above considerations suggest that the invasive gobies, as newly emerged and easily accessible prey, can influence trophic relationships in invaded ecosystems. However, the long-lasting effects of the gobies on populations of native predators and prey are more complex, difficult to predict, and this issue requires further research.

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Conflict of interest statement

The authors declare no conflict of interest

Author contributions

MA: Conceptualization, Resources, Formal analysis, Data interpretation, Visualization, Writing—Original draft preparation. KK: Investigation. JK: Conceptualization, Methodology, Investigation, Formal analysis, Writing—Original draft preparation. PH: Resources, Writing—Review & Editing. PK: Conceptualization, Writing—Review & Editing. MPK: Resources, Investigation, Writing—Review & Editing. ŁJ: Resources, Writing—Review & Editing. TK: Conceptualization, Methodology, Investigation, Writing—Original draft preparation Supervision, Funding acquisition.

Data availability

The data that support the findings of this study are available from the corresponding author, MA, upon request.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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