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# Does social context affect boldness in juveniles?

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## Abstract

Differences in boldness are common between populations or between related species and are discussed as part of individual coping style, personality, or behavioral syndrome. Boldness has been found to be dependent on experience, social, and environmental contexts. The major aim of the present study was to establish an experimental environment that would allow analyzing the risk-taking behavior of 2 competing invasive goby species. *Neogobius melanostomus* was more active in the absence of a predator *Sander lucioperca* than *N. fluviatilis* and clearly spent more time "swimming" and "feeding" than *N. fluviatilis*. In addition, *N. melanostomus* was always faster than *N. fluviatilis* both when leaving the shelter and reaching offered food. Based on the different behaviors recorded, species-specific boldness scores were established using a principal component analysis. Although there was no overall difference in boldness scores between the 2 species, both competitive conditions and the effect of the predator played significant roles as factors influencing boldness. *Neogobius melanostomus* was more affected by the presence/absence of the predator than the social circumstances. *Neogobius fluviatilis*, on the other hand, was more active and bolder in competitive situations. However, when alone, *N. fluviatilis* was rather inactive and displayed altogether shy behavior, independent of the presence/absence of the predator. Thus, the study confirms the prediction that there are differences in behavior and behavioral plasticity, and therein predator-avoidance strategies, between ecologically similar species of goby living in sympatry. We argue that these differences may be related to differential habitat use of both invasive species that presently dominate the fish community in the Lower Rhine.

Key words: boldness score, *Neogobius fluviatilis*, *Neogobius melanostomus*, predator-avoidance, social environment.

The study of boldness has been the focus of extended research in several animals like sparrows *Passer domesticus* (L. 1758) (Seress et al. 2011), sheep *Ovis canadensis* (Shaw 1804) (Reale and Fest-Bianchet 2003) or mice *Mus musculus* (L. 1758) (Sluyter et al. 1995), and, particularly fish, like Eurasian perch *Perca fluviatilis* (L. 1758), 3-spined stickleback *Gasterosteus aculeatus* (L. 1758), guppy *Poecilia reticulata* (Peters 1859), as well as sunfish *Lepomis gibbosus* (L. 1758) (reviewed by Sih et al. 2004). The underlying key aspect measured in all the behaviors above was the tendency to take on potential risks in the trade-off between foraging and safety constituting boldness. The tendency to be bold has been shown to be advantageous in processes like dispersal (Cote et al. 2010b; Wey et al. 2015) and invasion of new habitats (Chapple et al. 2012; Juette

et al. 2014) as well as in sexual selection (Godin and Dugatkin 1996 on guppies; Brodin et al. 2013 on frogs). Furthermore, it has been measured to be influential in the composition of groups (Magnhagen and Staffan 2005) and foraging efficiency (Ward et al. 2004).

Boldness has been found to vary with individual traits (e.g. age, sex, experience; Brown et al. 2005) and with social and environmental context (e.g. predation risk; Magnhagen and Borcherding 2008; Conrad et al. 2011; Goldenberg et al. 2014). Despite evidences that behavior patterns remain consistent over the course of ontogeny (Dingemanse et al. 2002), boldness has a fixed and a plastic component: boldness is known to vary with social context and with predation risk and is currently described as a personality trait. It is

therefore important to understand how stable boldness is and the factors shaping the expression of boldness in order to better understand its role in ecology (see also Utne and Aksnes 1994; Brown and Braithwaite 2004). For instance, some studies have shown that social behavior changes with environmental and developmental conditions (Bell and Stamps 2004).

Social context, that is, the formation of groups, plays an important role in the display of boldness behavior. Previous studies identified a group-effect on behavior in different species: Individual juvenile perch, examined in groups of either shy, bold, or intermediate temperament, were found to adapt their boldness level to that of their shoal mates (Magnhagen and Staffan 2005; Magnhagen and Bunnefeld 2009; Goldenberg et al. 2014). Individuals deemed shy and later put together with other shy individuals were observed to become bolder. Magnhagen and Bunnefeld (2009) noted that individuals who were comparatively bold were less likely to change their behavior under different social circumstances. Similarly, other studies on walleye pollock (*Theragra chalcogramma*, Baird and Olla 1991) and on cyprinids (Seghers 1981; Allan and Pitcher 1986) found strong evidence of an enhancement of boldness when group sizes increase.

Although adult gobies are benthic and do not form shoals as such, they are known to occur in high densities in the same habitat as juveniles in the Lower Rhine and are common prey to Percidae, such as the pikeperch *Sander lucioperca* (L. 1758) (Lindner 2014). This makes the influence of a group effect on gobiid behavior very likely. There is already some evidence of an adjustment of behavior in gobies under competitive as well as under predatory pressure (Borcherding et al. 2013a). Recent studies on invasive gobiid species at the Lower Rhine in Germany have dealt with activity patterns and competitive behavior in the round goby *Neogobius melanostomus* (Pallas 1814) and the bighead goby *Ponticola kessleri* (Günther 1861). These behavioral assays have indicated that adult *N. melanostomus* were more aggressive and territorial toward heterospecific intruders, but less bold than *P. kessleri*, this being estimated by the initiation of approaches and fights and the willingness to cross an exposed area to reach food (Borcherding et al. 2013b). The authors explained these behavioral differences by the competitive exclusion principle (Hardin 1960). As both species share similar habitats in the wild they were observed to consume different food sources and exhibit divergent behavioral patterns.

The aim of this study is to test the effect of social context and predation risk on the boldness of 2 ecologically similar, invasive species of goby. Since 2008, *N. melanostomus* and *N. fluviatilis* have spread from the Ponto-Caspian region to the Rhine and have developed in large numbers which already are threatening native fish diversity (Borcherding et al. 2011; Borcherding et al. 2013a; Gertzen et al. 2016). To be able to assess and evaluate their future invasive development in the establishment and spread stages of invasion (Blackburn et al. 2011), this study will compare a set of behavioral traits—culminating in boldness—known to assist in successful dispersal (Chapman et al. 2011a).

A boldness-score comprised of various behavioral features relevant to bold/shy responses, was used to compare the risk-taking behavior across intra- and inter-specific competition contexts in the presence or absence of a predator. The aim was to reveal specific behavioral traits and differences in predator-response strategies and discover potential context dependency of boldness and how it varies between species. According to the predictions of the competitive exclusion principle, it is hypothesized that there is a difference in behavior and, therein, boldness between *N. melanostomus* and the *N. fluviatilis*.

## Materials and Methods

### Fish collection and housing

Samples of gobies were collected on the 11 ($n = 28$) and 20 October 2011 ($n = 41$). Both species were caught either at a groyne field of the Rhine shore (842 km) or a nearby connected gravel pit lake near the field station where both species and their predators are known to occur (cf. Borcherding et al. 2013a; Gertzen et al. 2016). The fish were caught by means of beach seining with a 10 m × 1 m net with a mesh size of 1 mm. The total length of the tested individuals (Table 1) was measured to the nearest 1 mm. Sex determination had to be neglected due to the small body sizes.

Two holding tanks and 14 trial tanks (82 × 44 × 35 cm) were each filled with ca. 110 L of water (ca. 15 °C) from another nearby gravel pit lake (Reeser Meer) and the ground covered with 2 cm of sand-gravel substrate (Borcherding et al. 2013b). The backs and the sides were covered with black foil and 2 gray plastic boards served as lids for each tank. Both goby species were kept separately in the 2 holding tanks, fed with chironomid larvae every 2 days. They were kept and tested in a 10:14 h light:dark regime. Experimental tanks were positioned on metal shelves along which a black cloth with eyelets was hung to avoid distractions caused by the observer. One specimen of *S. lucioperca* (pikeperch) measuring 156 mm was caught also with beach seining and served as the predator in the experiments.

### Behavioral experiments

Experimental tanks were positioned on metal shelves along which a black cloth with eyelets was hung to avoid distractions caused by the observer. Randomly selected individuals for the experiments (number, species, and order see below) were transferred to the 14 trial tanks and always given 3 days to acclimate before the tests began. Acclimatization served as a means to accustom the gobies to the experimental conditions, which included the insertion and removal of a separating gray panel into and out of the tank (Milinski 1997). The panel divided the tank into 2 equally sized compartments which were needed during the pre-experimental period to separate the predator from the goby until the start of the recordings. During the acclimatization period, the panel was left in for approximately an hour once a day and carefully taken out after placing a small amount of chironomid larvae as food on the sand on the "predator-side" of the plate (Figure 1). Before each behavioral experiment, gobies were deprived of food 36 h prior to the start of testing to ensure insufficient hunger was not a factor influencing behavior. The experiments usually lasted from 8.30 AM to 2.30 PM. All behavioral recordings were conducted by the same observer to avoid

**Table 1.** Numbers and mean sizes of juvenile *Neogobius* species used in the different scenarios to test for boldness in our aquarium studies

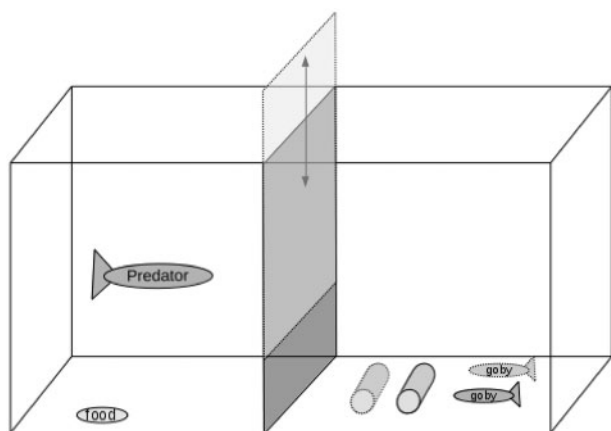| Scenario | *Neogobius fluviatilis* | | | *Neogobius melanostomus* | | |
| --- | --- | --- | --- | --- | --- | --- |
| | N | Mean TL | SD | n | Mean TL | SD |
| Single | 28 | 47.3 | 13.2 | 28 | 50.2 | 8.2 |
| Hetero-specific | 23 | 58.5 | 9.2 | 25 | 56.0 | 8.4 |
| Con-specific | 8 | 63.0 | 7.8 | 15 | 54.7 | 9.4 |

**Figure 1.** Experimental setup of the experimental tanks. Tanks were divided by an opaque panel into 2 compartments containing the predator on one side and gobies on the other. Removal of the panel marked the beginning of the trial period.

**Table 2.** Loadings of different behavioral measurements for 3 significant principal components explaining the majority of variance within the data set, based on the activity behaviors relevant to boldness which were incorporated in the analysis

|  | PC 1 | PC 2 | PC3 |
|---|---|---|---|
| Proportion of variance | 0.589 | 0.200 | 0.116 |
| Eigenvalue | 2.944 | 1.002 | 0.579 |
| Hiding | −0.462 | −0.499 | −0.044 |
| Latency emerge | −0.439 | −0.526 | −0.319 |
| Swimming | 0.451 | −0.106 | −0.776 |
| Latency feeding | −0.480 | 0.410 | 0.053 |
| Feeding | 0.399 | −0.543 | 0.540 |

multiple subjective biases. The experiment started with the introduction of the panel and the predator into the predator compartment (Figure 1, or the predator compartment remained empty). The observational period then began with taking the panel carefully out of the tank. With the help of the computer program "Perchmon" (see Borcherding and Magnhagen 2008) a set of behaviors was noted every second for 20 min for each individual, starting with the removal of the dividing panel. Four defined behaviors were noted when they had occurred yielding 1,200 data points per test bout for each individual fish. The recorded behaviors were defined as follows:

- "hiding": goby is located inside tube, until pelvic fin crosses tube entrance (or, seldom, burying in the sand = out of observer's sight).
- "swimming".
- "sitting": motionless lingering in 1 spot for more than 3 s.
- "feeding": lowering head to grab food and the following "chewing" movements of the jaws until swimming or sitting follows.

Behavioral tests on the first day were conducted in tanks either in the absence (7 tanks) or presence (7 tanks) of a predator, respectively, changing the predator presence on the next day. The effect of the sequence of predator introduction for all "single scenario" experiments were not significant so that this factor was excluded from further analyses (ANOVA, $P = 0.219$).

The 3 experiments consisted of a number of tests, each being a slightly modified version of the other.

## Experiment 1: behavior of single specimens

To assess behavioral responses of members of each species to the risk of predation without a competitive factor involved, 14 specimens of *N. fluviatilis* and 14 specimens of *N. melanostomus* were tested individually on 4 consecutive days. The experimental test tanks were always provided with 1 clay tube as shelter (diameter 2.5 cm, length 9 cm, manufactured by www.nature2aqua.de). Tests with *N. fluviatilis* were conducted on the first 2 days and those with *N. melanostomus* on the third and fourth day. This was done to keep testing times as closely together as possible to avoid temporal influences. One week later, the same tests were performed, however,

with *N. melanostomus* then being the species to be observed on the first and second day and *N. fluviatilis* on the third and fourth.

## Experiment 2: behavior of paired hetero-specifics

Fourteen specimens of each species were randomly selected from the holding tanks and roughly same-sized individuals put together in hetero-specific pairs. Equally sized pairs were necessary to avoid size-mediated dominance effects as the interest lay in the effect of an equal competitor on the behaviors in focus. After their acclimatization-period, 2 days of testing began during which the behaviors of both individuals were recorded.

One variation of Experiment 2 was conducted in the same interspecific competition/social contact context as before, however, this time, "shelter" was not a limiting factor by introducing a second clay tube in approximately the same distance to the food spot as the first. Eleven specimens of each species were paired with similar-sized hetero-specifics and the behavior of each specimen recorded. The sample size had to be adjusted to the decreased number of *N. fluviatilis* available. The effect of the number of tubes provided in the tanks for the experiments of the "hetero-specific scenario" proved to be insignificant (ANOVA, $P = 0.713$) and thus was disregarded in the further analysis.

## Experiment 3: behavior of paired con-specifics

For the tests involving intra-specific competition/social contact context, 5 pairs of *N. fluviatilis* and 8 pairs of *N. melanostomus* were observed using the same procedure as the hetero-specific pairs. The reduced sample sizes were due to a few cases of mortality in the holding tanks during the trial period. Specimens of a pair were again of matched sizes.

## Data analysis

Collected data were used to calculate the mean of each behavioral feature recorded for every individual as well as the total time needed to start moving/leave the shelter (latency to emerge) and the total time needed to begin feeding on chironomid larvae (first feeding event) after the dividing plate was removed (Supplementary Figure S1). By means of principal component analysis of all data from all 3 experimental scenarios it was possible to establish a boldness score using the component that explained most of the variance of the behavior (Table 2, cf. Magnhagen and Borcherding 2008).

To evaluate the impact of the different experimental factors on observed boldness scores, all potential factor combinations (covariate: size of individuals; species: *N. melanostomus*, *N. fluviatilis*; scenario: alone, hetero-specific, con-specific; predator: absence, presence) were tested in a linear model (Zuur et al. 2009), followed

by a Tukey HSD post hoc. The test for total length as covariate (ANCOVA, $P = 0.64$) was not significant so that size could be excluded from further analyses; this step was validated with a significant change of the Akaike information criterion in both models. The use of the ANOVA model was validated after positive results of the Bartlett Test of homogeneity of variance ($K$-squared = 19.002, df = 11, $P = 0.06106$). The model was also visually validated using the control plots of the ANOVA model showing the residuals versus fitted values and the standardized residuals versus theoretical quantiles (normal $Q$–$Q$ plot) (Zuur et al. 2009; see Supplementary Figure S2). As 3-factor-interactions are hardly to interpret, 2 ANOVA models were finally calculated for both species separately, to outline the interactions between the factors "Scenario" and "Predator" more clearly. All statistics were performed using the software R (Ver. 3.0.0, R Development Core Team 2009).

## Results

Using the observational data that depend on activity of the individuals (Supplementary Figure S1), a principal component analysis incorporating all data sets of Experiments 1, 2, and 3 yielded the following results (Table 2, all parameters except sitting). The first component explains approximately 59% of the total variation within the data set, where the parameters "hiding", "first feeding event", and "latency to emerge" generate negative values and "swimming" and "feeding" show positive loadings. As these loadings are in good correlation to an expected behavior along the bold–shy axis, we used PC1 as a boldness-score for each species in each of the 3 experimental scenarios.

Overall, the best model included the factors "Species", "Predator", and "Scenario" with all potential interaction terms, explaining roughly 43% of the total variance within the data set of PC1 for all experiments (Table 3). Although there was no evidence for a significant difference between the 2 species in overall boldness score regardless of social context or predatory risk ($P = 0.546$), the results of the ANOVA show that both social scenario as well as the presence/absence of a predator influenced overall boldness scores (both $P < 0.0001$). *Neogobius fluviatilis* reacted quite differently toward the presence of a predator (2-way ANOVA factor "Predator": $F = 23.3$, $P < 0.0001$) depending on the social context it was exposed to (Figure 2A, 2-way ANOVA factor "Scenario": $F = 48.2$,

**Table 3.** Results of an ANOVA (multiple *R*-squared: 0.429) testing overall differences on mean boldness score (PC1) of juvenile gobies with the factors "species" (*N. Fluviatilis* [nf], *N. Melanostomus* [nm]), "scenario" (single, con-specific, hetero-specific), and the presence or absence of a "predator" in our aquarium studies

|  | df | F | P |
| --- | --- | --- | --- |
| Species | 1 | 0.365 | 0.546 |
| Scenario | 2 | 35.23 | <0.0001 |
| Predator | 1 | 69.33 | <0.0001 |
| Species * scenario | 2 | 14.69 | <0.0001 |
| Species * predator | 1 | 1.420 | 0.235 |
| Scenario * predator | 2 | 0.415 | 0.661 |
| Species * scenario * predator | 2 | 4.355 | 0.014 |
| Residuals | 242 | | |

Notes: Differences between separate groups were tested with Tukey HSD post hoc comparisons of means, from which the 3-way-interactions are given in Supplementary Table S1.
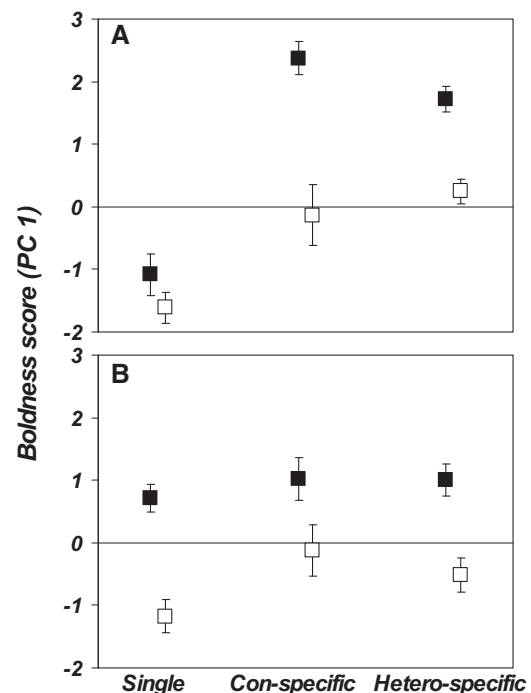
$P < 0.0001$). In single specimen experiments, *N. fluviatilis* did not show any change in boldness behavior whether exposed to a predator or not. However, boldness increased when paired with a conspecific (Tukey post hoc comparison of means, $P < 0.001$) and when paired with a hetero-specific (Tukey, $P < 0.001$) and decreased in the presence of the predator under intra-specific (Tukey, $P = 0.010$) and inter-specific competition (Tukey, $P = 0.012$, Table 3, 2-way ANOVA interaction term "Scenario" x "Predator": $F = 4.13$, $P = 0.0187$). *Neogobius melanostomus*, on the other hand, reacted strongly toward the presence of the predator (2-way ANOVA factor "Predator": $F = 47.0$, $P < 0.0001$), but did not differ in its boldness scores across social contexts (2-way ANOVA factor "Scenario": $F = 0.765$, $P = 0.467$). Overall, both species were bolder in presence of a predator when they had contact to another individual (of course less bold than in the absence of the predator), but only *N. fluviatilis* showed a marked increase in boldness score without predatory risk when placed in competition/social contact with other gobies (Figure 2; Tukey, with a con-specific: $P < 0.001$; with a hetero-specific: $P < 0.001$).

## Discussion

The first aim of the present study was to observe the risk-taking behavior of 2 competing goby species in the trade-off between feeding and predator avoidance. The obtained boldness score includes behavioral aspects such as "activity" and "delayed feeding attempts" which are related to boldness in other fish species (e.g., perch, Magnhagen and Borcherding 2008). Our results showed that there was no overall difference in boldness between the 2 species while social contexts and the presence of predators influenced boldness scores. Although an overall difference in boldness scores between the 2 species could not be found, both social scenario and the



**Figure 2.** Mean boldness score (PC1 ± standard error) of both gobiid species (A = *N. fluviatilis*, B = *N. melanostomus*) in the absence (black) and the presence (white) of a predator recorded during all experiments differing in social context.

effect of the predator played significant roles as factors influencing boldness in the experiments carried out. Besides further supporting the effectiveness of our measurements, together with the attained behavioral observations, 2 divergent strategies pursued by the 2 gobiid species can be discerned: N. melanostomus was more affected by the presence of a predator than by the social circumstances. In contrast to that, the results showed N. fluviatilis were active in social situations and rather inactive when alone. When tested in hetero-specific pairs, the reaction to the predator displayed by N. fluviatilis resembled that of N. melanostomus tested in competition with another specimen.

Recent studies have revealed a connection between sociality and boldness in fishes (Cote et al. 2010a; Conrad et al. 2011; Brown and Irving 2014; Jolles et al. 2015) and other species (Van Oers et al. 2005; Chapman et al. 2011b and reviewed by Webster and Ward 2011), which could explain the boldness reaction by N. fluviatilis to the social environment and relatively steady behavior across predator-absent or predator-present experiments that we observed. However, few studies have looked at the link between sociality and boldness and the reaction to predators (Keiser et al. 2015 on spiders; Cote et al. 2013 on fish), in which the strength of relationships between sociality and exploratory behavior (dispersal) or boldness varies with the predator presence. In their review, Conrad et al. (2011) explained how group movement in shoaling fish was led by bold, more socially indifferent individuals with greater exploratory tendencies being followed by shy, more socially sensitive individuals dependent on the effectiveness of the others' food allocation. This is supported by studies on sticklebacks and mosquitofish (Ward et al. 2004; Cote et al. 2010a). The same tendency was observed in the present study where N. fluviatilis appeared to have relied on N. melanostomus or a con-specific for their behavioral response. It would also imply that in direct comparison N. fluviatilis is less bold than N. melanostomus. The use of social information for foraging and predation avoidance has already been shown to exist in shoaling fish like perch (Magnhagen and Bunnefeld 2009) and sticklebacks (Coolen et al. 2003; Webster et al. 2007). Moreover, the transfer and use of public or social information among hetero-specifics of all taxa plays an important role in an individual's decision-making processes, especially when 2 species occupy similar ecological niches (reviewed by Goodale et al. 2010; see also Valone and Templeton 2002). Our results show that N. melanostomus was not affected by a social environment while N. fluviatilis relied more on public or social information and became more active and bolder when placed in a hetero- or con-specific environment.

Unlike N. fluviatilis, N. melanostomus reacted strongly toward the presence of the predator, while being rather unaffected by the change of the social context, as clearly revealed by the significant interaction term. A study on perch by Westerberg et al. (2004) revealed a correlation between boldness (time spent in the open) and competitive ability (number of pray attacks) in the presence of a predator. Although group members further affect an individual's behavior, results suggest that boldness and competitive ability, at least in con-specific groups, are related.

Magnhagen and Bunnefeld (2009) compared boldness of juvenile individuals by measuring their foraging behavior in the presence and absence of a predator when alone and in groups. They found that individuals were shyer when tested alone and became bolder when tested in groups and that individuals who were comparatively bold were less likely to change their behavior under different social circumstances. This "social impassiveness" was also apparent in N. melanostomus which was neither greatly affected by the presence of either hetero- or con-specifics, while frequently displaying territorial behavior typical of non-shoaling fish. Huntingford (1982) outlined a positive correlation between aggressiveness and boldness in 3-spined sticklebacks, suggesting a shared underlying cause with competitive ability (see Westerberg et al. 2004). The observed boldness and aggressiveness toward con- and hetero-specifics observed in the behavior of N. melanostomus (Hertel 2010, also observed in the present study, S. Loftus, personal observations) echo these findings.

Studies of juvenile perch examined groups of shy, bold, or intermediate temperament and found that they adapted their boldness level to that of their shoal mates. They observed that individuals deemed shy and later put together with other shy individuals became bolder (Magnhagen and Staffan 2005). Similarly, Goldenberg et al. (2014) observed a definite group-size effect in their study on boldness and vigilance behavior in young perch. Although our study was done on species-level, these results conform with our findings in the way that N. fluviatilis was also bolder when tested in pairs than when tested alone.

Possible explanations for the diverging behavioral strategies pursued by N. fluviatilis and N. melanostomus can be found in their choice of habitat in the Rhine. Regular sampling by the Ecological Research Station at the Lower Rhine have revealed that adult N. melanostomus occur both on rocky riprap revetments along the shores and on sandy substrates, frequently switching between both during foraging (Gertzen 2016). Neogobius fluviatilis on the other hand is solely found on gravel and sand (Borcherding et al. 2013a). Neogobius melanostomus therefore is not as much dependent on the safety provided by a group-effect as N. fluviatilis is in open surroundings, but can escape back between the rocks when a predator approaches. On gravel and sand, however, N. fluviatilis has fewer opportunities to find cover from predators and, therefore, individuals become an easy prey when they are alone. Thus, they rather rely on the group-effect to dilute the per capita predation risk. This enhances competitive interactions and also provides them with public information about food location which can lead to increased foraging activity. This effect was evident in the experiments conducted in this study when N. fluviatilis remained almost inactive throughout all single scenarios tests while showing a marked increase in activity and, therein, boldness during paired scenario tests. The findings of the present study confirm our prediction that there are behavioral differences between the 2 studied ecologically similar species of goby living in sympatry in the Lower Rhine. Our study shows that a species' boldness behavior can vary with social contexts or not. Context-consistency and context-specificity of boldness were formerly shown to exist only on individual-level in sticklebacks, sunfish (context-consistency: Ward et al. 2004; Webster et al. 2009; context-specificity: Coleman and Wilson 1998; Webster et al. 2007 in sunfish) and between separate populations of the same species (Bell 2005; Borcherding and Magnhagen 2008 in perch). The results we produced show this to be true also on species-level where 2 species sharing a common habitat as juveniles apply divergent behavioral response strategies to predation risk, in accordance with the competitive exclusion principle (Hardin 1960).

## Ethical standards

After the experimental period, all surviving fish were released at their capture site. The experiments complied with the current laws of Germany and were approved by the ethic commission of the University of Cologne.

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## Supplementary material

Supplementary material can be found at http://www.cz.oxfordjournals.org/.

## References

Allan JR, Pitcher TJ, 1986. Species segregation during predator evasion in cyprinid fish shoals. *Freshwat Biol* **16**:653–659.

Baird TA, Olla BL, 1991. Social and reproductive behavior of a captive group of walleye pollock *Theragra chalcogramma*. *Environ Biol Fish* **30**:295–301.

Bell AM, 2005. Behavioural differences between individuals and two populations of stickleback *Gasterosteus aculeatus*. *J Evol Biol* **18**:464–473.

Bell AM, Stamps JA, 2004. Development of behavioural differences between individuals and populations of sticklebacks *Gasterosteus aculeatus*. *Anim Behav* **68**:1339–1348.

Blackburn TM, Pysek P, Bacher S, Carlton JT, Duncan RP et al., 2011. A proposed unified framework for biological invasions. *Trends Ecol Evol* **26**:333–339.

Borcherding J, Dolina M, Heermann L, Knutzen P, Krüger S et al., 2013a. Feeding and niche differentiation in three invasive gobies in the Lower Rhine, Germany. *Limnologica* **43**:49–58.

Borcherding J, Hertel A, Breiden S, 2013b. Activity and competitive behaviour of invasive *Neogobius melanostomus* and *Ponticola kessleri* (Gobiidae) from the River Rhine, Germany. *Ethol Ecol Evol* **25**:351–365.

Borcherding J, Magnhagen C, 2008. Food abundance affects both morphology and behaviour of juvenile perch. *Ecol Freshwat Fish* **17**:207–218.

Borcherding J, Staas S, Krüger S, Ondrackova M, Slapansky L et al., 2011. Non-native Gobiid species in the lower River Rhine (Germany): recent range extensions and densities. *J Appl Ichthyol* **27**:153–155.

Brodin T, Lind MI, Wiberg MK, Johansson F, 2013. Personality trait differences between mainland and island populations in the common frog *Rana temporaria*. *Behav Ecol Sociobiol* **67**:135–143.

Brown C, Braithwaite VA, 2004. Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcopi*. *Anim Behav* **68**:1325–1329.

Brown C, Irving E, 2014. Individual personality traits influence group exploration in a feral guppy population. *Behav Ecol* **25**:95–101.

Brown C, Jones F, Braithwaite VA, 2005. In situ examination of boldness–shyness traits in the tropical poeciliid *Brachyraphis episcopi*. *Anim Behav* **70**:1003–1009.

Chapman BB, Hulthen K, Blomqvist DR, Hansson LA, Nilsson JA et al., 2011a. To boldly go: individual differences in boldness influence migratory tendency. *Ecol Lett* **14**:871–876.

Chapman BB, Thain H, Coughlin J, Hughes WOH, 2011b. Behavioural syndromes at multiple scales in Myrmica ants. *Anim Behav* **82**:391–397.

Chapple DG, Simmonds SM, Wong BBM, 2012. Can behavioral and personality traits influence the success of unintentional species introductions? *Trends Ecol Evol* **27**:57–64.

Coleman K, Wilson DS, 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim Behav* **56**:927–936.

Conrad J, Weinersmith K, Brodin T, Saltz J, Sih A, 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *J Fish Biol* **78**:395–435.

Coolen I, van Bergen Y, Day RL, Laland KN, 2003. Species difference in adaptive use of public information in sticklebacks. *Proc R Soc B* **270**:2413–2419.

Cote J, Clobert J, Brodin T, Fogarty S, Sih A, 2010a. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philos Trans R Soc Lond B Biol Sci* **365**:4065–4076.

Cote J, Fogarty S, Tymen B, Sih A, Brodin T, 2013. Personality-dependent dispersal cancelled under predation risk. *Proc R Soc B* **280**:20132349.

Cote J, Fogarty S, Weinersmith K, Brodin T, Sih A, 2010b. Personality traits and dispersal tendency in the invasive mosquitofish *Gambusia affinis*. *Proc R Soc B* **277**:1571–1579.

Dingemanse NJ, Both C, Drent PJ, Van Oers K, Van Noordwijk AJ, 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim Behav* **64**:929–938.

Gertzen S, 2016. The ecological niche of invasive gobies at the lower rhine in intra- and interspecific competitive and predatory interactions [PhD thesis]. University of Cologne, 205 pp.

Gertzen S, Fidler A, Kreische F, Kwabek L, Schwamborn V et al., 2016. Reproductive strategies of three invasive Gobiidae co-occurring in the Lower Rhine (Germany). *Limnologica* **56**:39–48.

Godin JGJ, Dugatkin LA, 1996. Female mating preference for bold males in the guppy *Poecilia reticulata*. *Proc Natl Acad Sci USA* **93**:10262–10267.

Goldenberg SU, Borcherding J, Heynen M, 2014. Balancing the response to predation: the effects of shoal size, predation risk and habituation on behavior of juvenile perch. *Behav Ecol Sociobiol* **68**:989–998.

Goodale E, Beauchamp G, Magrath RD, Nieh JC, Ruxton GD, 2010. Interspecific information transfer influences animal community structure. *Trends Ecol Evol* **25**:354–361.

Hardin G, 1960. The competitive exclusion principle. *Science* **131**:1292–1297.

Hertel A, 2010. Activity patterns and behavior of the invasive fish species *Neogobius melanostomus* [bachelor thesis]. University of Cologne, 63.

Huntingford FA, 1982. Do interspecific and intraspecific aggression vary in relation to predation pressure in sticklebacks? *Anim Behav* **30**:909–916.

Jolles JW, Fleetwood-Wilson A, Nakayama S, Stumpe MC, Johnstone RA et al., 2015. The role of social attraction and its link with boldness in the collective movements of three-spined sticklebacks. *Anim Behav* **99**:147–153.

Juette T, Cucherousset J, Cote J, 2014. Animal personality and the ecological impacts of freshwater non-native species. *Curr Zool* **60**:417–427.

Keiser CN, Wright CM, Pruitt JN, 2015. Warring arthropod societies: social spider colonies can delay annihilation by predatory ants via reduced apparency and increased group size. *Behav Process* **119**:14–21.

Lindner J, 2014. Stomach analyses of 0+ predators in the lower Rhine: Perch *Perca fluviatilis*, Pikeperch *Sander lucioperca*, Ruffe *Gymnocephalus cernuus* and Asp *Aspius aspius* [bachelor thesis]. University of Cologne, 102.

Magnhagen C, Borcherding J, 2008. Risk-taking behaviour in foraging perch: does predation pressure influence age-specific boldness?. *Anim Behav* **75**:509–517.

Magnhagen C, Bunnefeld N, 2009. Express your personality or go along with the group: what determines the behaviour of shoaling perch? *Proc R Soc B* **276**:3369–3375.

Magnhagen C, Staffan F, 2005. Is boldness affected by group composition in young-of-the-year perch *Perca fluviatilis*? *Behav Ecol Sociobiol* **57**:295–303.

Milinski M, 1997. How to avoid seven deadly sins in the study of behavior. *Adv Study Behav* **26**:159–180.

R Development Core Team, 2009. *R: A Language and Environment for Statistical Computing*. Vienna (Austria): R Foundation for Statistical Computing (ISBN 3-900051-07-0).

Reale D, Fest-Bianchet M, 2003. Predator-induced natural selection on temperament in bighorn ewes. *Anim Behav* **65**:463–470.

Seghers BH, 1981. Facultative schooling behavior in the spottail shiner *Notropis hudsonius*: possible costs and benefits. *Environ Biol Fish* **6**:21–24.

Seress G, Bokony V, Heszberger J, Liker A, 2011. Response to predation risk in urban and rural house sparrows. *Ethology* **117**:896–907.

Sih A, Bell A, Johnson JC, 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* **19**:372–378.

Sluyter F, Bult A, Lynch CB, Vanoortmerssen GA, Koolhaas JM, 1995. A comparison between house mouse lines selected for attack latency or nest-building: evidence for a genetic basis of alternative behavioral strategies. *Bahav Genet* **25**:247–252.

Utne ACW, Aksnes DL, 1994. An experimental-study on the influence of feeding versus predation risk in the habitat choice of juvenile and adult 2-spotted goby *Gobiusculus flavescens* (Fabricius). *J Exp Mar Biol Ecol* **179**:69–79.

Valone TJ, Templeton JJ, 2002. Public information for the assessment of quality: a widespread social phenomenon. *Philos Trans R Soc Lond B Biol Sci* **357**:1549–1557.

Van Oers K, de Jong G, van Noordwijk AJ, Kempenaers B, Drent PJ, 2005. Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour* **142**:1185–1206.

Ward AJW, Thomas P, Hart PJB, Krause J, 2004. Correlates of boldness in three-spined sticklebacks *Gasterosteus aculeatus*. *Behav Ecol Sociobiol* **55**:561–568.

Webster MM, Ward AJW, 2011. Personality and social context. *Biol Rev* **86**:759–773.

Webster MM, Ward AJW, Hart PJB, 2007. Boldness is influenced by social context in three-spine sticklebacks *Gasterosteus aculeatus*. *Behaviour* **144**:351–371.

Webster MM, Ward AJW, Hart PJB, 2009. Individual boldness affects inter-specific interactions in sticklebacks. *Behav Ecol Sociobiol* **63**:511–520.

Westerberg M, Staffan F, Magnhagen C, 2004. Influence of predation risk on individual competitive ability and growth in Eurasian perch, *Perca fluviatilis*. *Anim Behav* **67**:273–279.

Wey TW, Spiegel O, Montiglio PO, Mabry KE, 2015. Natal dispersal in a social landscape: considering individual behavioral phenotypes and social environment in dispersal ecology. *Curr Zool* **61**:543–556.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM, 2009. *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer Verlag.