The aggressive personality of an introduced fish affects foraging behavior in a polymorphic newt

Abbreviated title: Effect of fish personality on amphibians

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The study of personality has aroused much interest and has provided insight into the understanding of animal behavior. Nevertheless, the study of the ecological consequences of personality is a newer field that could shed light on cases of alien species introductions. The goldfish (*Carassius auratus*) is frequently introduced worldwide and affects the abundance of newts, having an especially negative impact on an alternative phenotype, the paedomorph, which maintains larval traits at the adult stage, unlike the other phenotype, the metamorph, which has undergone metamorphosis. We experimentally assessed the impact of goldfish on the foraging behavior of both phenotypes of palmate newts (*Lissotriton helveticus*). More particularly, we assessed fish personality by analyzing the foraging activity and the aggressiveness toward newts, and newt personality by analyzing individual difference in boldness. In the presence of fish, fewer newts foraged than in their absence, and paedomorphs were more affected than metamorphs. We found strong personality differences in fish and fewer newts foraged in the presence of a more aggressive fish. Newts differed in boldness, but fish aggressiveness remains a key factor to explain newt behavior. Studying behavioral interactions between native and alien species helps to understand the mechanisms of coexistence and exclusion and why different phenotypes might be affected differently by the same threat. To a great extent, not only the presence of fish alters the foraging opportunities of newts but also the personality of the invader; integrating personality patterns of invaders is therefore a key to understanding the ecological consequences of alien species introduction.

Key words: amphibian, behavioral type, ecological consequence, foraging behavior, invasive species, paedomorphosis, polymorphism, temperament.

INTRODUCTION

The concept of personality in animals has been increasingly developed within the last decade (Sih et al. 2004a, 2004b). Animal personality, also called behavioral type, refers to behavioral variation among individuals that is consistent over time (Biro and Stamps 2008; Carter et al. 2013). Personality traits (i.e., behavioral traits) such as activity, aggression and boldness represent specific aspects of the behavioral repertoire, which vary among individuals but are

consistent within an individual (Carter et al. 2013). The concept of behavioral syndrome extends to the correlation between 2 or more personality traits over time in either the same basic context or across environmental situations (Sih and Bell 2008; Stamps and Groothuis 2010). The existence of animal personality has been reported in a wide variety of taxa, such as insects (Niemelä et al. 2012), amphibians (Koprivnikar et al. 2012), fish (Conrad et al. 2011), birds (van Overveld et al. 2014) and mammals (Favreau et al. 2014).

Although the existence of personality traits throughout the animal kingdom has been relatively well established (Stamps and Groothuis, 2010), the ecological consequences of these variations have received much less attention (Wolf and Weissing 2012). The ecological consequences of animal personalities can be relatively easily assessed in predator–prey interactions. Depending on the context, active and bold individuals can be favored or disadvantaged in a highly predatory environment (Brydges et al. 2008; Archard and Braithwaite 2011). The divergence of patterns found across studies shows the complexity of behavioral trait evolution (Carlson and Langkilde 2014). Nevertheless, the selection of a behavioral trait, such as boldness in prey might also depend on the behavior of predators (Smith and Blumstein 2008; Pruitt et al. 2012). Indeed, in predator–prey interactions, behavioral traits of both predator and prey influence the outcome of species interactions (McGhee et al. 2013). However, in many studies on predator–prey interactions, the predator is often considered as a fixed and unresponsive threat, rather than as an agent that can display behavioral plasticity and have its own adaptive pressure (Lima 2002). In a foraging context, however, the predator activity level, which is one of the most widely studied personality traits (Careau et al. 2008), should influence predator–prey encounters (Toscano and Griffen 2014). Moreover, bolder predators tend to spend more time searching for prey, and approach them faster and have a higher rate of predatory success after detection (Ioannou et al. 2008). The risk experienced by prey might then be determined by the personality type of predators.

Differences in individual behavior are relevant in the introduction of alien species. Indeed, the establishment process of alien species depends on their behavior: successfully introduced species can often outcompete native species for food and habitat, but they also exhibit high levels of interspecific aggression (Holway and Suarez 1999; Chapple et al. 2012). Differences in competitive ability between alien and native species can thus determine the coexistence or the exclusion of these species. Moreover, the impact of alien species is especially strong, because native species must often learn to recognize a potential predator and adopt strategies to respond successfully to the level of threat (Ferrari and Chivers 2011; Sih et al. 2012). Suitable responses are particularly important, because strategies such as avoidance behavior can protect potential prey from predation, but also reduce essential activities such as foraging (Lima and Dill 1990; Lima and Bednekoff 1999).

The goldfish (*Carassius auratus*) is the most frequently introduced ornamental fish in the world (Savini et al. 2010). The aquarium trade and pet stores have been identified as the principal source of goldfish introduction in the natural environment (Maceda-Veiga et al. 2013). The goldfish is considered as invasive, particularly due to its extreme tolerance to environmental stress (Abramenko et al. 1997), which allows the species to occupy a wide variety of habitats (Gherardi 2007; Lorenzoni et al. 2010), including small ponds used by amphibians such as newts (Denoël et al. 2013). Goldfish are predators of salamander eggs and larvae (Monello and Wright 2001), but have not been reported to prey on the adult stage because of gape-size limitation. However, they cause avoidance behavior and reduce foraging and sexual behavior in adult newts in laboratory conditions (Winandy and Denoël 2013a, 2013b), suggesting that newts perceive them as a threat. In the field, goldfish affect newt populations by limiting their occurrence and decreasing their abundance (Denoël and Ficetola 2014).

Therefore, in addition to the general disturbance caused by goldfish introduction, competition for food can be problematic, because goldfish are omnivorous (Sales and Janssens 2003) and their diet can overlap with that of native amphibians (Richardson et al. 1995). However, the mechanisms involved in exclusion or persistence remain unknown and how different fish personalities can influence avoidance behavior of native amphibian species has never been studied.

A widespread polymorphism in newts and salamanders is facultative paedomorphosis (Denoël, Joly et al. 2005). This results in the coexistence of alternative phenotypes in populations: whereas one undergoes metamorphosis (the metamorph), the other phenotype retains larval traits, such as gills at the adult stage (the paedomorph), and remains completely aquatic. Paedomorphosis has some advantages in allowing resource partitioning in deep and heterogeneous habitats (Whiteman et al. 1996; Denoël et al. 2004) and precocious maturation (Ryan and Semlitsch 1998; Denoël and Joly 2000). The expression of each phenotype is dependent on environmental variables (see review in Denoël, Joly et al. 2005), but also on a quantitative trait locus, as was recently shown in ambystomatid salamanders (Voss et al. 2012). The paedomorphic phenotype is more sensitive to fish introduction than the metamorphic phenotype: paedomorphs occur less frequently in fish ponds than metamorphs. When coexisting with goldfish, paedomorphs are often less abundant than metamorphs, but the reasons remain unknown (Denoël, Džukić et al. 2005; Denoël and Ficetola 2014). Paedomorphs are thought to be more vulnerable because they cannot escape water and often forage in the same microhabitats as fish (Denoël, Džukić et al. 2005). Beyond these hypotheses, no experiments to date have tested the different behavioral responses of metamorphs and paedomorphs towards fish.

In this context, the aim of this study was to assess: 1) the impact of goldfish presence on newt foraging behavior, considering the 2 newt phenotypes; 2) the individual differences in goldfish behavior (i.e., personality) when newts are foraging and the individual differences in newt boldness (i.e., foraging in a risky area), and 3) the impact of fish personality on newt foraging. Referring to these objectives, our hypotheses were 1) that the 2 phenotypes forage less in the presence than in the absence of fish, but with a stronger impact on paedomorphs, 2) that all goldfish do not exhibit the same feeding activity level and are not equally aggressive toward newts, and that newts do not exhibit the same level of boldness, and 3) that fewer newts forage in a tank with more active and aggressive goldfish.

MATERIALS AND METHODS

Study organism

The goldfish were obtained from a fish retailer (Blue Coral, Herstal, Belgium, provider of the Aquarium of the University of Liège). Before the beginning of the experiment, the fish were maintained in a large tank (180 × 80 cm², 60-cm water depth) at a mean temperature of 18°C and a photoperiod of 11 h light/13 h dark. The goldfish had a mean (± standard error [SE]) total length of 11.8 ± 0.2 cm and a weight of 22.7 ± 0.8 g ($n = 12$).

We caught 96 palmate newts (48 metamorphs and 48 paedomorphs with 24 individuals of each sex) by dip-netting in a pond devoid of fish ("Le Coulet North-East," Larzac Plateau, France) on 29 March 2013. Capture took place early in the reproduction period. At the time of collection, the population consisted of 49% metamorphs ($n = 331$). We stored newts (keeping morphs and sex separate) for 1 day in 4 large tanks (80 × 40 cm², 20-cm water depth), before

bringing them to the laboratory in 6, 3-L tanks ($30 \times 20 \times 18$ cm^3) placed in a refrigerated box (230 L).

Laboratory maintenance

On 31 March 2013, we distributed the newts among 24 identical and independent tanks (60×60 cm^2, 40-cm water level; 135 L) with 4 individuals (one of each sex and each phenotype) per tank. Goldfish were placed simultaneously in 12 out of the 24 experimental newt tanks. We covered the bottom of the tanks with pieces of slate. In each fish tank, goldfish were in direct contact with newts, but we provided newts with 1 large shelter (20×60 cm^2) closed by a grid to prevent the fish from entering. The same type of shelter was also available in the control tanks without fish. An oxygen diffuser was placed in each tank. The ambient air temperature was regulated and controlled every day to maintain the water temperature at a mean of 14.69°C (SE = 0.05°C). We established a photoperiod (with 1 Lumilux de lux 2350-lm daylight tube, L36W/12-950, and 1 Sylvania Professional tube, 36W DECOR183) that reflected the natural cycle at the capture location (12 h light/12 h dark). Newts were fed with 50 mg of thawed *Chironomus* larvae per newt every day in the afternoon, which represent a typical newt prey and the quantity provided corresponded to the newts' needs. Goldfish began to receive the same food as the newts 1 month before the beginning of the study, to avoid detection and the effects of diet cues (Chivers and Smith 1998) on the newts. During the study period, at the end of each day (after the experiments), 200 mg of thawed *Chironomus* larvae was provided to the goldfish at the surface of the water so that newts did not use it (goldfish consumed food rapidly).

Experimental procedure

To assess the impact of fish presence on newt foraging, we compared the 24 experimental tanks (newts and fish remained in their original tanks throughout the study period): 12 tanks as a control treatment with the absence of fish and 12 tanks in the presence of fish. Thawed *Chironomus* larvae (200 mg per tank, i.e., about 40 larvae) were placed on the bottom of each tank. A cylindrical cage (20-cm high, 20 cm in diameter and 2.5-cm mesh size) was placed above the food to prevent fish from eating it (Figure 1). The feeding cage was in direct contact with the shelter of the tanks, so that newts could choose to fully avoid the fish. The cage was removed when all the food was consumed.

Foraging data collection consisted of focal observation (Martin and Bateson 2007) performed in the late afternoon. We assessed individual foraging behavior ($n = 96$) by determining which newts fed on *Chironomus* larvae (1 = foraging and 0 = no foraging) and the latency to foraging of each newt (the time from food delivery to the first feeding act of a newt, measured with a chronometer). The same observer, located 2 m from the aquaria, recorded these behavioral patterns. Newts did not react to the observer during this procedure. We could easily distinguish each newt, because there was only 1 individual of each sex and phenotype in each tank. The focal sampling ended when all newts in a tank ate, or when all food items were foraged. The foraging data collection was conducted for each tank once a week for 12 weeks, but newts were fed in the same way on each day of the experiment.

Figure 1 Experimental design for the feeding experiment: a cylindrical cage was placed above the food at the bottom of the tanks. Palmate newts, but not the goldfish, can pass through the grid to forage on thawed *Chironomus* larvae.
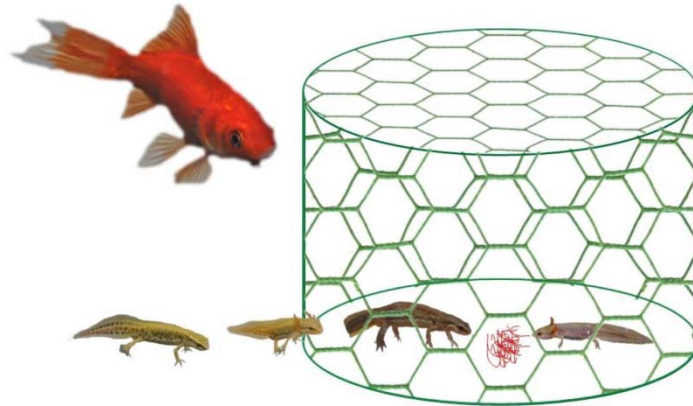
We analyzed fish personality during newt feeding by recording fish behavior in each tank where a goldfish was present ($n = 12$) for 15 min (starting from the introduction of the food) using a video camera (Sony HDR-CX730E and HDR-HC3E, Sony Corporation, Japan) placed in front of each tank. By watching at the video files on a computer, we examined 2 behavioral patterns to assess individual variation in fish personality. Firstly, we assessed the foraging activity level of the fish by calculating the proportion of time spent by fish around the feeding area: that is, when the fish was swimming around the grid. We scored the proportion of this activity pattern with a scan-sampling method (Martin and Bateson 2007), which consists of instantaneous sampling of the individual at set time intervals and the type of activity of the individual at the moment of the scan is recorded. Observation was based on 15 scans of each fish, recorded every minute for 15 min (for each scan, we scored 1 = activity around the feeding area, 0 = swimming only elsewhere in the tank). The swimming behavior around the feeding cage could be interpreted as foraging activity, because fish were very attracted by *Chironomus* larvae and moved to swim around the grid after the introduction of food into the cage. We expected that the presence of fish close to the feeding area might stress the newts that might therefore avoid this area. Secondly, we characterized the aggressive behavior of the fish toward newts by analyzing the number of pecking behaviors, i.e., when the fish sucked a part of the newt body during the 15-min observation period. Goldfish are benthic feeders that suck food on the bottom and expel what cannot be eaten (Smith and Gray 2011). Therefore, pecking behavior can be interpreted as a predatory attack: aroused by the presence of food, the fish tried to eat the newts, which were too large to enter their mouths. Fish were able to peck newts when they were outside the grid or sometimes through it. Even if it was harmless (no newts were wounded), we presume that this pecking behavior was perceived as an attack by the newts. This "pecking" variable was calculated from the number of pecks divided by the number of newts that were present around the feeding area and were available to be pecked, to obtain the number of pecks per newt. This was obtained by recording the presence of newts over the whole 15-min period. We also recorded which newt phenotype (i.e., paedomorph or metamorph) was pecked. Finally, since newt personality might also explain foraging behavior, we also tested the potential existence of individual differences in newt feeding behavior. Boldness can be defined as the expression of a behavior under a potential risky condition (Réale et al. 2007). Because the foraging behavior of newts can be considered risky, given the possible encounter with fish,

we assessed newt boldness by assessing their feeding activity (1 = foraging and 0 = no foraging). We also assessed the existence of newt personality on each phenotype separately.

To assess the consistency in individuals over time, data collection on newt and fish behavior was repeated 3 times in different weeks during the last 3 weeks of the experiment. We chose to experiment during the final weeks, to avoid the novelty aspect, when both fish and newts had become accustomed to the feeding process, because learning and habituation can influence repeatability when assessing animal personality (Réale et al., 2007). Moreover, after several weeks, the newt latency to feeding was strongly reduced compared with that at the beginning of the experiment; therefore, 15 min of recording was sufficient to assess fish and newt interactions. In total, we generated 36 videos (9 h of recording). All data were collected by only 1 observer.

Statistical analysis

We used a generalized linear mixed model (GLMM) to test the effect of fish presence and newt phenotype across 4 treatments (metamorphs in the presence of fish, metamorphs without fish, paedomorphs in the presence of fish, and paedomorphs without fish) and over time (12 weeks of data collection as the ordinal variable) on 1) the proportion of foraging newts (using binomial error distribution) and 2) the latency to forage (using log-normal distribution). To take into account the dependency of the data, we included individuals and tanks as a random factor: individuals nested within tanks (Pinheiro and Bates 2000). Significance was assessed using likelihood-ratio tests (ANOVA of the model with a particular explanatory variable vs. the model without that variable). We also used a Tukey contrast test to assess significant differences between the 4 treatments. To focus on the effect of phenotype and fish, we did not include the sex of the newts in the models. Separate GLMM analyses confirmed that sex had no significant effect on the studied behaviors: the proportion of foraging newts (n = 96 newts, χ^2_1 = 0.63, P = 0.43) and the latency to forage (n = 96 newts, χ^2_1 = 0.58, P = 0.45).

To analyse fish personality (i.e., to assess whether the 12 fish in the experiment behaved similarly or whether they showed individual differences), we first used a global linear model (GLM) (F-test) to assess the effect of individuals, time (3 weeks of data collection as ordinal variable) and interaction between individuals and time on 1) the proportion of foraging activity during newt feeding (this variable was transformed using the square-root arcsine to satisfy the assumption of normality) and 2) on aggressive behavior (pecking). By running this type of model, significant variation in individual behavior, combined with the absence of an interaction between individual and time, would indicate that individuals differ in the way they respond and that this difference is constant over time (Réale et al. 2007). We also estimated the repeatability in feeding activity and aggressiveness using a linear mixed effects model with the restricted maximum likelihood procedure (Nakagawa and Schielzeth 2010). We tested the relationship between individual variation in feeding activity and individual difference in aggressive behavior using an F-test. Finally, we used a GLM to test the effect of phenotype on aggression to assess whether fish equally pecked metamorphs and paedomorphs.

To assess the impact of fish personality traits on newt foraging (n = 48), we used a linear regression to test the effect of each fish personality score (the mean proportion of feeding activity and the mean number of pecking) on the proportion of foraging newts per tank (this variable was transformed using the square-root arcsine to satisfy the assumption of normality). Because there was no significant difference in the mean proportion of foraging newts during the first 9 weeks or during the last 3 weeks, that is, when fish personality was assessed (GLMM

including tank as a random factor: $n = 12$, $\chi^2_1 = 1.45$, $P = 0.23$), we tested the effects of fish personality scores on the mean proportion of foraging newts during the entire 12-week period of the experiment.

Because both fish and newts can differ in personality, we also tested for individual differences in newt boldness (foraging behavior in a risky area). We used a GLM to test the potential effect of individuals, time (with 3 weeks of data collection as an ordinal variable) and their interaction on newt foraging behavior. We introduced several covariables into the model, which might affect the expression of newt personality: the phenotype, fish activity score and fish pecking score. We also estimated repeatabilities (for binomial data) for both phenotypes separately, using the same methods as for fish. Finally, we tested the impact of fish personality score (activity and pecking) on newt foraging using a GLMM, taking into consideration the phenotype as a covariable and newt individuals as a random effect.

We chose an *a priori* level of significance of 0.05. Analyses were performed in R 3.0.2 (www.r-project.org) using the lme4, multcomp, and rptR packages.

Ethical note

The aim of this study was to determine only the potential nonconsumptive effects of goldfish on adult newts by observing their foraging behavior. Consequently, care was taken to plan the experiment accordingly and to avoid any risk of wounds to newts. This study mimics natural conditions in wild and garden ponds, where goldfish are introduced and coexist with newts (Denoël and Ficetola 2014). The research was conducted in a licensed University of Liège laboratory (LA1610429), and the research project was accepted by the university's Animal Ethics Commission (Protocol No. 1246). The collecting permit was issued by the Direction régionale de l'Environnement, de l'Aménagement et du Logement (DREAL) Languedoc-Roussillon. In the laboratory, all individuals were monitored and fed daily. At the end of the experiment, all newts remained alive and were not wounded, and were released into their capture habitat following the recommendations of the capture permit. All materials used for capture and maintenance were thoroughly washed and disinfected before and after use, following the recommendations of the study permit.

RESULTS

Effect of fish presence on newt foraging

There was a significant effect of treatment on the proportion of foraging newts ($n = 96$ newts, $\chi^2_3 = 19.25$, $P < 0.001$, Figure 2): Tukey contrast tests revealed significant differences between metamorphs in the presence of fish and control metamorphs ($Z = -3.9$, $P < 0.001$) and between paedomorphs in the presence of fish and control paedomorphs ($Z = -5.31$, $P < 0.001$). Fewer newts of both phenotypes foraged in the presence than in the absence of fish. There was also a significant difference between metamorphs in the presence of fish and paedomorphs in the presence of fish ($Z = -2.81$, $P = 0.02$), showing that fewer paedomorphs foraged than metamorphs in the presence of fish. There was no significant effect between metamorphs and paedomorphs in the control treatment ($Z = -1.355$, $P = 0.51$). There was a significant effect of

time (12 weeks of data collection as an ordinal variable) on the proportion of foraging newts (n = 96 newts, χ^2_1 = 14.49, $P < 0.001$), showing variation across weeks in the proportion of newts that foraged. There was no significant interaction between time and treatment (n = 96 newts, χ^2_3 = 1.63, P = 0.65).

Figure 2 Foraging behavior of the 2 phenotypes of palmate newts (n = 96: 48 metamorphs and 48 paedormophs) in control or fish treatment (mean ± SE) (n = 24 tanks). See Results for statistical analysis. * $P < 0.05$, *** $P < 0.001$.
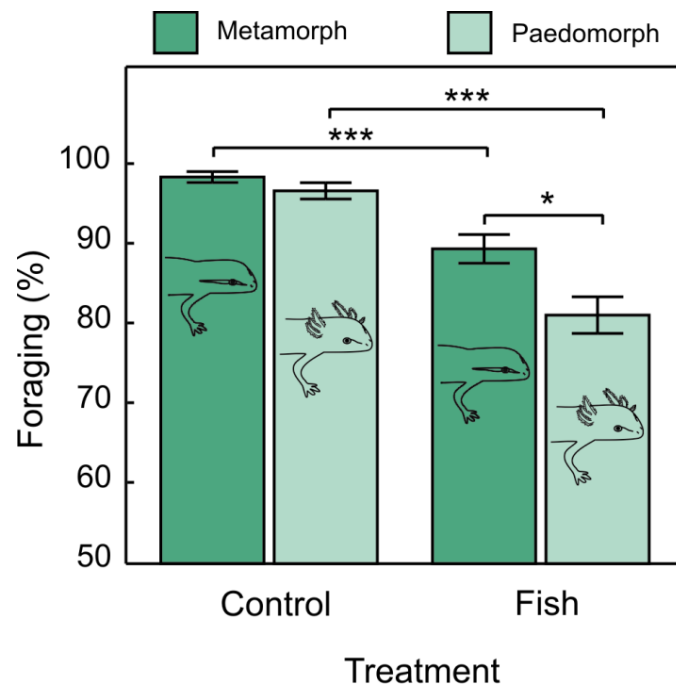
There were no significant effects of treatment on the latency of newt foraging (n = 96 newts, χ^2_3 = 0.82, P = 0.85). However, there was a significant effect of time (n = 96 newts, χ^2_1 = 63.09, $P < 0.001$), with longer latency values during the first than the final few weeks. There was also a significant interaction between treatment and time (n = 96 newts, χ^2_3 = 43.11, $P < 0.001$): although the latency to foraging gradually decreased in the control group of metamorphs and paedomorphs, it varied during the first 5 weeks in the fish groups of metamorphs and paedomorphs (Figure 3).

Figure 3 Newt latency to forage (*n* = 96: 48 metamorphs and 48 paedormophs) across treatment (fish and control, *n* = 24 tanks) and over time (mean ± SE). See Results for statistical analysis.
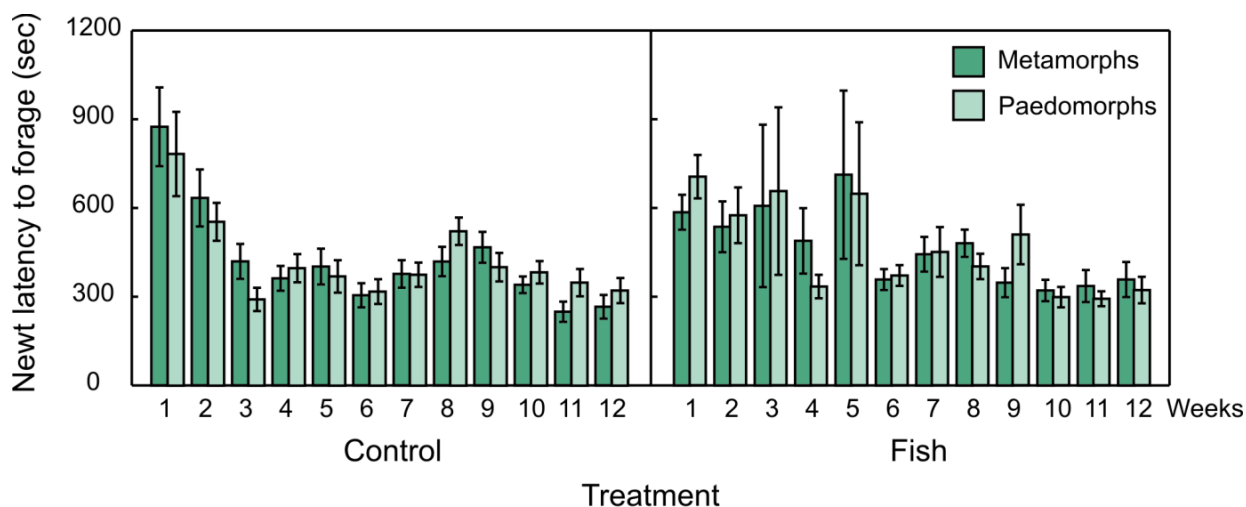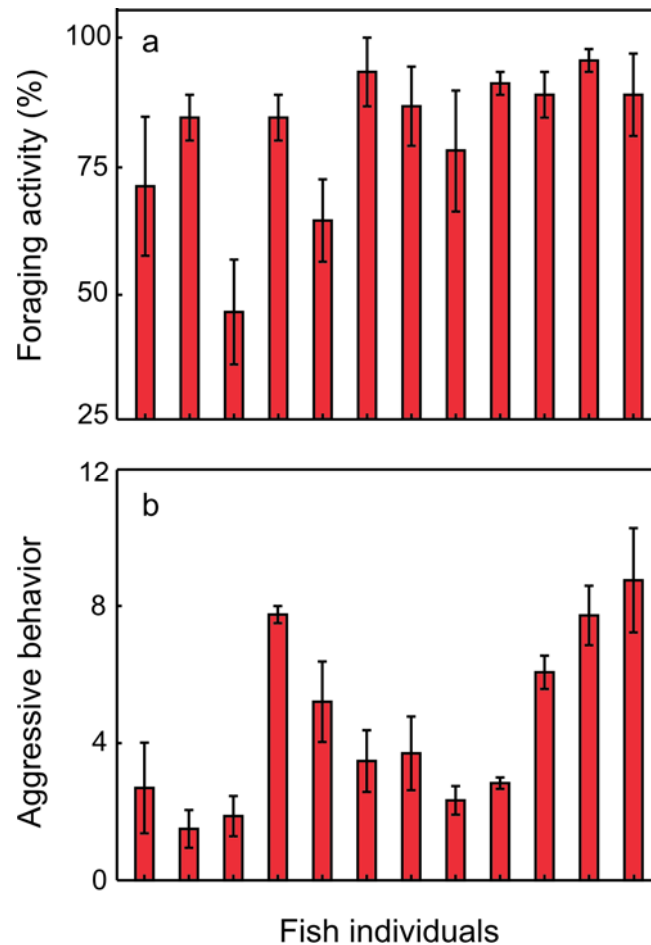

Fish personality traits

We found considerable variability in foraging activity and aggressive behavior among fish individuals (Figure 4). Fish were active surrounding the feeding area for a mean proportion of 81.50% ± 2.95 (SE) of the 15-min observation time. Fish attacked (i.e., pecked) each newt 4.4 ± 0.5 times. There was a strong significant effect of individuals (*n* = 12) on foraging activity and on aggressive behavior (Table 1). For these 2 variables, individual behavior was consistent over time: there were no significant effects of time (3 weeks of data collection as an ordinal variable) and no interaction between individual and time (Table 1). The repeatability estimate was moderate for feeding activity ($R = 0.43$, SE = 0.18, $P = 0.001$) and high for aggressiveness ($R = 0.7$, SE = 0.15, $P < 0.001$). Feeding activity and aggressive behavior were not significantly correlated ($R^2 = 0.14$, $F_{1,10} = 1.64$, $P = 0.23$).

Table 1 GLMs to evaluate the effect of individual, time (ordinal variable), and their interaction on foraging activity and aggressive behavior of fish (pecking newts) (*n* = 12 fish)

Fish personality traits	Effects	*F*	d.f.	*P*
Foraging activity	Individual	2.4	11,22	**0.04**
	Time	0.51	1,22	0.48
	Individual x Time	1	11,22	0.49
Aggressive behavior	Individual	7.44	11,22	**<0.001**
	Time	0.59	1,22	0.45
	Individual x Time	0.37	11,22	0.94

Significant values are highlighted in bold. df = degrees of freedom.

Figure 4 Fish individual variation in the percentage of foraging activity (a) and on aggressive behavior during newt feeding; score based on the number of pecks per newt (b). Values are means ± SE. Each bar represents a different fish individual ($n = 12$). See Results and Table 1 for statistical analysis.

Impact of fish personality on newt foraging

There was no significant effect of fish feeding activity on the proportion of foraging newts per tank ($R^2 = 0.03$, $F_{1,10} = 0.29$, $P = 0.6$). There was a significant effect of fish aggressive behavior on newt foraging ($R^2 = 0.48$, $F_{1,10} = 9.25$, $P = 0.01$, Figure 5): in the presence of a more aggressive fish, fewer newts foraged. Finally, there was no significant effect of phenotype on fish aggressive behavior ($F_{1,69} = 0.08$, $P = 0.78$): fish pecked metamorphs and paedomorphs equally (mean ± SE = 3.6 ± 0.72 and 3.9 ± 0.79, respectively).

Figure 5 Relationship between the proportion of foraging palmate newts and the aggressive personality of goldfish (score based on the mean number of pecks per newt). The dotted lines show the 95% confidence interval. See Results for statistical analyses.
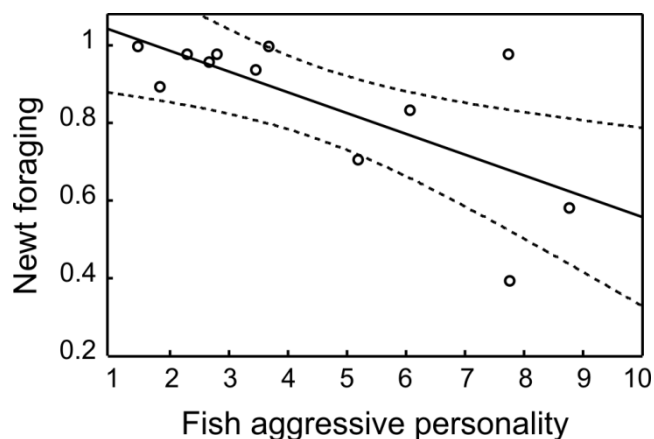
Effect of newt personality trait (boldness)

Considering the effect of fish personality (activity and pecking scores) and phenotype as covariables, there was a significant effect of newt individual ($n = 48$) on boldness, that is, feeding in a risky area ($F_{47,89} = 2.37$, $P < 0.01$) meaning that all newts did not exhibit the same level of boldness. Individual behavior was consistent over time: there were no significant effects of time ($F_{1,89} = 1.9$, $P = 0.18$) or of the interaction between individual and time ($F_{47,89} = 0.87$, $P = 0.69$). Repeatability was observed for both paedomorphs ($R = 0.51$, SE $= 0.12$, $P = 0.001$) and metamorphs ($R = 0.46$, SE $= 0.16$, $P = 0.01$). When we considered phenotype and newt individuals, there was still a significant effect of fish aggressive personality ($\chi^2_1 = 14.15$, $P < 0.001$), no significant effects of fish activity ($\chi^2_1 = 0.04$, $P = 0.85$) and no significant interactions between fish personality and phenotype ($\chi^2_1 = 0.83$, $P = 0.36$ and $\chi^2_1 = 2.3$, $P = 0.13$ for aggression and activity, respectively), suggesting that both metamorphs and paedomorphs were affected by fish aggression, but not by fish activity.

DISCUSSION

The results showed that the personality traits of an introduced fish help to explain the behavior of native newts: the more aggressive a fish was, the less the newts foraged. Moreover, different newt phenotypes responded differently to the presence of fish; paedomorphs avoided foraging in a risky area more than metamorphs. These experimental results agree with field data that showed variation patterns across newt populations into which fish were introduced and where one of the 2 phenotypes was more affected than the other (Denoël and Ficetola 2014). Studying personality can thus help to understand the ecological consequences of alien species introduction (Wolf and Weissing 2012), especially considering the level of aggression in a predatory or competitive context (Pintor et al. 2008, 2009).

Effect of fish presence on paedomorphic and metamorphic foraging newts

During the 3 months of the experiment, fewer newts foraged in the presence of fish than in their absence. Similar patterns of avoidance behavior have been reported for fish (Leahy et al. 2011), birds (Sorato et al. 2012), mammals (Eccard and Liesenjohann 2008) and other amphibians (Watson et al. 2004). The detrimental impact of fish on newts is understandable, because many amphibians typically evolve in aquatic habitats naturally devoid of fish (Cox and Lima 2006; Salo et al. 2007; Leu et al. 2009). This extends previous experimental results that showed the impact of goldfish on the survival of eggs and larvae of long-toed salamanders (Monello and Wright 2001) as well as on feeding and breeding opportunities in alpine newts (*Ichthyosaura alpestris*) (Winandy and Denoël 2013b).

In contrast to previous studies on the effect of fish on amphibians (Winandy and Denoël 2013a, 2013b), we determined the effect of fish on 2 different newt phenotypes. We found that both phenotypes did not respond to fish presence in the same way: whereas as many paedomorphs as metamorphs foraged in the absence of fish, fewer paedomorphs than metamorphs foraged in the presence of fish. Even if both phenotypes were affected by fish, this shows that paedomorphs responded more than metamorphs to the potential threat caused by fish. However, neither paedomorphs nor metamorphs were preyed on by goldfish and the fish pecked equally frequently at both phenotypes. These observations lead to the hypothesis that some paedomorph traits make them more vulnerable than metamorphs. Due to their smaller size than metamorphs (Denoël et al. 2009), the pecking might be more stressful. Additionally, paedomorphs might be more fragile than metamorphs, given their external gills and their thinner skin (Andreone et al. 1993), making them more sensitive to fish and thus more responsive to avoid contact. Moreover, the greater avoidance of danger by paedomorphs than metamorphs can also be explained by a difference in coping style (i.e., strategies used to deal with a stressful situation) between the 2 phenotypes. As has been shown for fish, the coping style can be predicted by the degree of fearfulness (Martins et al. 2011). Paedomorphs might therefore exhibit more fear and consequently greater avoidance concerning a potential threat than metamorphs. The lower foraging activity of paedomorphs than metamorphs in the presence of fish is expected to be costly and might in part explain the rare coexistence of paedomorphs and fish in the wild (Denoël and Ficetola 2014), as well as the observed decline in paedomorph populations after fish introductions (Denoël, Džukić et al. 2005). A decrease in foraging activity is particularly detrimental, because it could reduce growth (Relyea 2002; Teplitsky et al. 2003) and fecundity (DeWitt et al. 1998).

Latency to foraging decreased over time in newts, as was shown previously (Winandy and Denoël 2011), but here, we showed that newts reacted differently in the presence of fish. Indeed, in the control group, latency strongly decreased in the second week whereas the latency of the fish group only decreased in the fifth week. This delay in latency reduction might be explained by the novelty of fish disturbance: newts might learn how to cope with fish encounters to reach the feeding area. This process can take time and implies decision-making through risk assessment (Ferrari et al. 2010). Indeed, an effective anti-predator response implies correct risk assessment with adjustment and readjustment of the response (Ferrari et al. 2005).

Fish personality traits

This study highlights that goldfish differ in different personality traits. Both foraging activity and aggression toward newts were dependent on fish individuals and were stable throughout the experiment. Most fish individuals were continuously swimming around the grid when food

was provided, whereas others were not present around the food source. Because this experiment took place in a familiar environment with a familiar procedure to the fish, this activity did not reflect an exploration of a novelty situation, but a directed behavior toward food (Réale et al. 2007). This activity near food can be interpreted as feeding motivation, because more active fish are trying to obtain food. This is not surprising, because the degree of foraging activity is associated with the metabolic rate (Careau et al. 2008) and food intake (Biro and Stamps 2008). It has been shown that northern pike (*Esox lucius*) with higher metabolic rates are able to pursue prey actively, rather than using an ambush strategy (McGhee et al. 2013). Moreover, goldfish are voracious and their omnivorous diet (Richardson et al. 1995) can even lead them to gluttony when food is in abundance (Balon 1977).

In this study, the aggressive behavior of fish towards newts can be considered as an attempt at predatory aggression driven by appetite mechanisms (Olivier and Young 2002). The results showed strong individual variation in aggression toward newts, with a high repeatability score. In the presence of food, some fish pecked newts whenever they had the opportunity, that is, when newts were outside the shelter to approach the food source, whereas other fish were not aggressive at all. Aggressiveness can therefore be used to gain access to resources. Because this behavioral trait can facilitate foraging success (Stamps 2007), it can also positively affect survival (Smith and Blumstein 2008).

In invasive species, a high level of foraging activity and aggression is essential for competition during establishment, leading to a strong impact on native species. Indeed, these 2 behavioral traits allow the high feeding and growth rates in introduced species to be maintained, which makes individual invaders more numerous and successful and thereby strongly able to impact the native communities (Pintor et al. 2009). The existence of different personalities among an introduced species is also important for its persistence in the invaded environment: although more active and aggressive personalities are better competitors, they are also more vulnerable to predation than less active personalities, showing that different personalities can be selected, depending on the ecological context (Brown et al. 2014; González-Bernal et al. 2014).

Contrary to our expectation, there was no correlation between the level of foraging activity and aggression: the most active fish in the feeding area were not necessarily the most aggressive toward newts. Although aggressiveness and activity had been classified as two distinct personality traits (Réale et al. 2007), a correlation between the traits suggests a behavioral syndrome (Sih and Bell 2008); indeed, an aggression syndrome based on the correlation between foraging activity and aggressiveness has been reported for the invasive crayfish and leads to high attack rates on native species (Pintor et al. 2009). However, it has also been shown for other species, that activity and aggressiveness are not part of the same syndrome: altough activity is often correlated with exploratory behavior, aggressiveness is more often associated with boldness (Moretz et al. 2007). Moreover, a meta-analysis of correlated behavioral traits showed a weak relationship between aggression and activity, demonstrating the complexity behind correlating behavioral traits (Garamszegi et al. 2013).

Impact of fish personality traits on newt foraging

We found no impact of fish foraging activity on the number of foraging newts. Thus, the nearby presence of fish swimming actively around the feeding area did not prevent newts from reaching food. We cannot exclude that newts were habituated to the fish presence and assessed the risk to still have the opportunity to eat (Winandy and Denoël 2013a). However, a fish with a

particularly aggressive personality that pecked newts several times caused newts to remain in their shelter, to avoid the risk of an encounter that might lead to a direct attack. Indeed, goldfish can catch a part of the newt's body and briefly prevent the newt from escaping. The absence of an effect of fish foraging activity and the strong effect of fish pecking on new foraging confirms that this is the direct interaction with fish that could be detrimental and avoided by newts. By minimizing their foraging opportunities, a potential prey reduces the chance of being detected and attacked by predators, and this is particularly the case when the risk is high (Lima and Dill 1990). A recent study also showed that bolder predators spent more time searching for prey and consequently caught more prey (Ioannou et al. 2008). Thus, if a species shows variation in boldness and aggression, the risk experienced by prey can therefore be determined by these predator traits. Moreover, in a foraging context, the activity level of predators and prey should influence their encounter rate (Sweeney et al. 2013). Nevertheless, by avoiding threatening encounters, potential prey pays the cost of foraging less (Semlitsch 1987). Therefore, coexistence with a potential predator or aggressive competitor implies trade-offs between behaviors such as foraging and the risk of being attacked (Horat and Semlitsch 1994; Bridges 2002).

Effect of newt boldness

There was a difference in newt boldness for individuals of both phenotypes and this variation was stable over time. Bolder newts foraged despite the risk of an encounter with fish. Although this behavior is expected to be costly in terms of survival, due to the risk of predatory attacks, more active and bolder individuals might attain a higher foraging and mating success (Biro and Stamps 2008; Smith and Blumstein 2008; DiRienzo et al. 2013). Therefore, the maintenance of variation in boldness within populations can potentially be explained by the trade-off hypothesis, where individual fitness depends on the environmental context, such as the risk of predation (Sih et al. 2004b). In our study, even when variation between individual newts was considered, we still observed a strong impact of aggressive fish personality on newt foraging, showing that fish aggressiveness remains a key factor to explain newt behavior.

CONCLUSIONS

Individual variations in the behavior of alien species such as goldfish can be crucial for their establishment success (Wolf and Weissing 2012). Aggressiveness and high foraging rates of invaders might allow them to outcompete native species, leading to their extirpation (Pintor et al. 2008). Even if goldfish are not considered as predators of adult newts, their presence has been associated with both newt population disappearance, or with a sharp decrease in newt abundance (Denoël, Džukić et al. 2005). The consequence of goldfish introduction is particularly harmful for the paedomorphic newt phenotype (Denoël and Ficetola 2014), suggesting that the palmate newt can coexist with this fish, but at the cost of intraspecific diversity loss. Both the presence of micro-habitats (providing shelter) and the fish species (predatory or not predatory) have been highlighted as factors in the understanding of coexistence and exclusion mechanisms between introduced fish and native amphibians (Hartel et al. 2007). Here, we showed that inter-individual variation in behavior might also be a key factor in determining the outcome of species interactions (Sweeney et al. 2013). Specifically, aggressiveness, together with foraging voracity and boldness, is essential behavioral mechanisms related to the superior competitive behavior of introduced species compared with

native species (Gamradt et al. 1997; Pintor et al. 2008, 2009). This demonstrates that future studies should consider the personality of the invader when assessing the ecological consequences of alien species introduction (Pintor et al. 2008), as far as individual variation in the ability to cope with novel threat within the invaded community (Blake and Gabor 2014). Indeed, in predator–prey interactions, both the personality of predator and prey can influence the outcome of their interaction (Pruitt et al. 2012; McGhee et al. 2013).

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