Animal Behaviour 138 (2018) 157–164

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Defence is the best offence: invasive prey behaviour is more important than native predator behaviour

Gloria J. Mennen, Kate L. Laskowski*

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

ARTICLE INFO

Article history:
Received 14 November 2017
Initial acceptance 15 January 2018
Final acceptance 2 February 2018

MS. number: 17-00903

Keywords:
Dikerogammarus villosus
foraging
Gammarus roeseli
invasion syndrome
predator–prey interactions

Finding universal rules that predict the success of potential invaders is difficult given the breadth of interactions that occur between the invader and the other species in its new range. Among animal species, behavioural traits may play an especially relevant role in mediating these interactions. Whereas the predatory behaviour of invasive predators is especially well documented, less is known about how behaviour may mediate the success of invasive prey species. Here we tested how the behaviour of both an invasive prey species, the amphipod *Dikerogammarus villosus*, and a common fish predator, the European perch, *Perca fluviatilis*, affect the outcome of predation events. Invasive *D. villosus* exhibited significantly greater sheltering and less exploratory behaviour than a naturalized amphipod *Gammarus roeseli*. This increased sheltering behaviour in the invasive amphipod appears to have a major functional consequence as this species was far less likely than the naturalized amphipod to be predated by the perch. Contrary to our predictions, the behaviour of the individual perch had no influence on consumption of either amphipod species, suggesting that amphipod behaviour was the key determinant of the success of a predation event. Our results highlight the importance of prey behaviour during predation events and emphasize that consideration of antipredator behaviour in potentially invasive prey species may help improve predictions of invasion success.

Invasions are an increasing problem in our globalized world. Predicting whether an invasive species will be able to successfully spread, become established and cause problems in its new range is difficult. Many traits such as abiotic tolerance, life history strategies and behavioural traits (reviewed in Hayes & Barry, 2008) are known to contribute to invasion success. However, finding universal rules that predict a potential invader's success is hampered by the fact that each invasion event is characterized by a unique set of interactions between the invader and the native community. Given its flexibility, behaviour may be especially relevant during the invasion process (Carere & Gherardi, 2013; Chapple, Simmonds, & Wong, 2012; Holway & Suarez, 1999) when an invading animal needs to be able to reach and then persist in its new environment. However, it is still unclear which behaviours might be most beneficial to invaders, although trophic position (i.e. the amount of predation it will experience) can help predict the nature of the interactions an invader will have with the resident community. Many invasive animal species exhibit a suite of behavioural characteristics that have been implicated in helping potential invaders disperse further (Rehage & Sih, 2004), outcompete native species (Duckworth & Badyaev, 2007) and increase consumption rates (Bollache, Dick, Farnsworth, & Montgomery, 2008; Pintor, Sih, & Bauer, 2008). In general, many invasive species are found to show higher levels of activity, aggression, exploration and/or sociability than native or resident species (Duckworth & Badyaev, 2007; Hudina, Hock, & žganec, 2014; Monceau, Moreau, Poidatz, Bonnard, & Thiéry, 2015; Pintor et al., 2008; Rehage & Sih, 2004). These behaviours are especially obvious in invasive species that lack predators in their invasive range (e.g. lionfish, *Pterois volitans*: Green, Akins, Maljković, & Côté, 2012; cane toads, *Rhinella marina*: Shine, 2010). However, many invaders occupy lower trophic levels and a key step to their successful invasion is likely to be avoidance of consumption by predators. For these invaders, more passive behaviours may be more beneficial if they help reduce invader visibility and predator encounter rates (Briffa, Jones, & MacNeil, 2016; De Gelder et al., 2016; Truhlar & Aldridge, 2015); however, so far invader behaviour in the face of predation has received considerably less attention making it unclear how important behaviour in this context is for invasion success.

* Correspondence: K.L. Laskowski, Leibniz-Institute of Freshwater Ecology & Inland Fisheries, Department of Biology & Ecology of Fishes, Müggelseedamm 310, 12587 Berlin, Germany.
E-mail address: kate.laskowski@gmail.com (K. L. Laskowski).

https://doi.org/10.1016/j.anbehav.2018.02.017
0003-3472/

Prey behaviour is only one half of the equation as predator behaviour will also play a key role in any predation event. Predators can be important at stopping or limiting the spread of invaders from lower trophic levels (Reusch, 1998; Salo, Nordström, Thomson, & Korpimäki, 2008; Sheehy & Lawton, 2014; Smith, 2006) and the behaviour of individual predators may be especially relevant as they are often able to consume multiple prey within a short time. However, even within the same population not all predators can be considered equivalent (Bell, Hankison, & Laskowski, 2009). There are now several examples where repeatable behavioural differences between individual predators, that is, their personality or behavioural type, have been shown to influence which prey an individual predator will be most successful at attacking and consuming (Belgrad & Griffen, 2016; DiRienzo, Pruitt, & Hedrick, 2013; Pruitt, Stachowicz, & Sih, 2012; Royauté & Pruitt, 2015; Sweeney et al., 2013). In general, bolder and more active predators appear to have greater success at capturing less active prey (Pruitt et al., 2012; Sweeney et al., 2013). These behavioural traits may additionally be important when a predator encounters a novel and (potentially) invasive prey if boldness increases a predator's likelihood of encountering and consuming the prey species. Thus, understanding the interplay between prey and individual predator behaviour should improve our predictions of the success of a potential invasive prey species.

The freshwater amphipod *Dikerogammarus villosus*, native to the Ponto-Caspian region, is now rapidly invading throughout western Europe (Bij de Vaate, Jazdzewski, Ketelaars, Gollasch, & Van der Velde, 2002). In Germany, this species began invading relatively recently with the opening of the Main-Danube canal in 1992 (Rewicz, Grabowski, MacNeil, & Bacela-Spychalska, 2014). *Dikerogammarus villosus* exhibits a suite of traits that appear to make it an ideal invader (reviewed in Rewicz et al., 2014). For example, it exhibits high tolerance to a broad range of abiotic conditions (Bruijs, Kelleher, Van der Velde, & De Vaate, 2001; Wijnhoven, Van Riel, & Van der Velde, 2003), has a high reproductive capacity (Devin, Piscart, Beisel, & Moreteau, 2004; Pöckl, 2009) and fast growth rate (Piscart, Devin, Beisel, & Moreteau, 2003). Importantly, its behaviour also plays a key role in its success. *Dikerogammarus villosus* is highly aggressive and exerts significant predation pressure on lower trophic levels, allowing it to outcompete resident amphipod species (Bollache et al., 2008; Dick & Platvoet, 2000; MacNeil & Platvoet, 2005) and leading to decreases in local biodiversity (Van Riel et al., 2006). These behaviours suggest that, at least in a competitive context, *D. villosus* exhibits the increased aggression and activity characteristic of many invasive species. However, less is known about how this amphipod behaves when, instead, it is the target of predation (but see Briffa et al., 2016; De Gelder et al., 2016; Truhlar & Aldridge, 2015) where active and aggressive behaviour may actually increase the amphipod's visibility and encounter rates with its own predators.

Here we tested how the behaviour of both the invasive *D. villosus* and a common fish predator, the European perch, *Perca fluviatilis*, influences the outcome of predation events between these two species. To determine whether *D. villosus*'s behaviour is similar to that of other amphipod species or a potentially unique contributor to its invasion success, we compared the behaviour of *D. villosus* to that of *Gammarus roeseli*. After its invasion of Europe over 150 years ago, *G. roeseli* populations appear to have stabilized and it is now considered a 'naturalized' species (Josens et al., 2005). We compared these two species as we expected that comparing an 'old invader' with a newer one would help control for potential differences in other traits (e.g. life history) allowing us to better isolate the effects of behavioural differences. Additionally, *G. roeseli* and *D. villosus* co-occur at our study sites and are morphologically similar in size and shape. Given the incredibly high densities that *D. villosus* appears to achieve in its invasive range, we expected that individual level behaviour may be less important than species level differences between the two amphipod species. However, as perch are capable of consuming many amphipods at a time, we expected that individual perch behaviour might be especially relevant for their interactions with the amphipods. Thus, our goals were (1) to compare average behaviour between the species *D. villosus* and *G. roeseli*, (2) to determine whether individual perch differed consistently in their own behaviour and (3) to determine how the behaviour of the predator and prey contributed to the outcome of predation events between individual perch and groups of either single or mixed species of amphipods. Based on results found in other invasive species (Duckworth & Badyaev, 2007; Hudina et al., 2014; Monceau et al., 2015; Pintor et al., 2008; Rehage & Sih, 2004), we predicted that *D. villosus* would exhibit more active and exploratory behaviour than the naturalized *G. roeseli*. We additionally predicted that individual perch that were more active and bolder should be more successful at consuming the invasive *D. villosus*.

METHODS

Animal Collection and Maintenance

Amphipods were opportunistically collected from Lake Müggelsee and nearby streams around Berlin, Germany in summer 2016. After collection, amphipods were housed in single-species aquaria at our laboratory (tank volume = 244 litres). Holding aquaria contained gravel, leaf litter and wooden logs similar to those found at the collecting sites. Amphipods were fed daily with plant-based fish food and thawed frozen bloodworms. We used adult amphipods that had been acclimated to the laboratory for at least 1 week and were of similar size (mean ± SE = 13.1 ± 0.8 mm) for all experiments. We could not distinguish between the sexes but avoided using individuals that were engaged in the clasping and mate-guarding behaviour typical of individuals about to moult and mate.

Perch were collected from Lake Müggelsee using a sink net in June 2016. All perch were about 1 year old and were not yet sexually dimorphic preventing us from sexing them. Upon capture, fish were anaesthetized (1 ml/litre 9:1 ethanol:clove oil solution in about 5 litres of lake water) and marked with a unique combination of three colours of subcutaneous UV elastomer at three spots on their anterior side to allow permanent individual identification. Fish recovered in a dark aerated bucket and swam normally within about 15 min. All fish survived the procedure and showed no adverse effects. Perch were housed in four large (about 400 litres) aquaria in groups and fed an ab libitum diet of thawed frozen bloodworms twice daily for approximately 6 weeks prior to the start of the experiments (the first foraging trials began at the end of July). We used a total of 24 perch for our experiments.

Amphipod Behavioural Assays

We assessed two behaviours that we predicted could be relevant both for the amphipods' invasion ability and their ability to avoid or escape predation: hiding and activity behaviour in a familiar environment and exploration in a novel environment. To measure behaviour in a familiar environment, we placed groups ($N = 10$ individuals per aquarium; 10 aquaria per species) of a single species in small (tank volume = 3 litres) aquaria each containing a single wooden log (roughly 10 cm long and 5 cm in diameter) similar to their holding tanks. The amphipods settled (and were not fed) for 24 h after which time we counted the amphipods (out of 10) engaged in hiding, feeding or mating behaviour six times over the