

Editorial**Behaviour and Aquatic Invasions in the 21st Century: Progress, Trends and Future Research**Kit Magellan^{1,*}, Mhairi Alexander², Amy Deacon³ and Marian Wong⁴¹University of Battambang, Cambodia²University of the West of Scotland, United Kingdom³The University of the West Indies, St Augustine, Trinidad and Tobago⁴University of Woolongong, Australia

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Welcome to the Behaviour and Invasions Special Issue of *Aquatic Invasions*. In the 20 years since Holway and Suarez (1999) issued their plea for behavioural analyses to be more fully integrated into invasion studies, have things changed, and if so how? This Special Issue was conceived because behaviour seemed rarely to be the focus of studies of biological invasions: at *Aquatic Invasions* we received only two or three behavioural submissions per year (KM *pers. obs.*). This is a critical oversight as behaviour is central to understanding how animals interact with their environment, which is particularly important in species introductions. This may also suggest that progress in the field of behaviour and invasions is limited, but the papers in this Special Issue show how much this field has evolved over the last 20 years. The 11 papers presented here cover behavioural topics ranging from predator-prey interactions through competition to learning, and focus on fish, amphibian and invertebrate model species. However, perhaps the most striking pattern is geographical. The research for this Special Issue, together with the invasive model species, encompasses both Northern and Southern hemispheres and spans six continents from Asia to the Americas, with mostly multinational author teams. Behaviour and invasions is a truly global field of research.

The most common theme of this Special Issue is predator-prey behaviour, aspects of which are the focus of five papers. This is an important consideration for biological invasions: introduced species usually do not share an evolutionary history with the novel species in their invaded habitat which may enable them to exploit vulnerable native prey species or mean they become naïve prey themselves (Sih et al. 2010). We open with Levri et al. (2019), who examined floating behaviour in different clones of the New Zealand mud snail, *Potamopyrgus antipodarum*, which has invaded several water bodies in the U.S.A. These snails are able to float up

and attach themselves to the water surface via surface tension. In response to odour from unknown predators, all tested populations exhibited this behaviour, though native populations tended to carry out less floating behaviour. The authors speculate that dispersal via floating may partially explain the invasion success of the most common invasive clones in the U.S.A. (Levri et al. 2019).

Three of the papers in this issue focus on invasive amphibian prey species. Kruger et al. (2019) investigated the behaviour of the invasive African clawed frog, *Xenopus laevis*, in France. They show that naïve *X. laevis* tadpoles innately reduced their activity with predator stimuli but not with a neutral stimulus. Moreover, this reaction occurred regardless of the degree of relatedness between the tested predators and predators within the frog's native range. Although it is unknown whether this response reflects a long-term evolutionary process in the native range, a rapid *in situ* response that evolved in the invaded range, or a generic anti-predator defence, this ability to respond appropriately to unknown predators will certainly promote the invasive success of *X. laevis* (Kruger et al. 2019). Chuang et al. (2019) examined another pervasive invasive anuran, the American bullfrog, *Lithobates catesbeianus*, in Korea. The authors describe how *L. catesbeianus* tadpoles increased their survival with a native predator by hiding in a submerged vegetation refuge. They also demonstrate that this behaviour is plastic: while all tadpoles preferred submerged vegetation only those subject to a simulated predator attack also preferentially used floating vegetation. Tadpoles can thus modify their behaviour based on previous experience (Chuang et al. 2019). Greenlees and Shine (2019) take a different approach by focusing on how native predatory frogs, *Litoria dahlii*, may survive the invasion of a hazardous prey species, toxic cane toads, *Rhinella marina*, in Australia. They show that exposure to cane toad tadpoles induced learned aversion in native frogs, which carries over to avoidance of more toxic metamorph cane toads (Greenlees and Shine 2019).

The final predator-prey paper also initiates the second representative taxonomic group of this Special Issue, the Poeciliidae. This family of small live-bearing fishes includes a number of global invaders, most famously the guppy, *Poecilia reticulata*, and the mosquitofish, *Gambusia affinis*, the latter being one of the world's 100 worst invasives (Lowe et al. 2004). Brodin et al. (2019) assessed how different behaviour types of mosquitofish vary in their predator survival at low densities. The authors show that asocial individuals were better able to survive predation than social ones. Asocial individuals may also be more likely to disperse suggesting that the invasion front for mosquitofish populations consists of capable dispersers who are likely to survive predation (Brodin et al. 2019).

The next two poeciliid papers both examine a specific branch of predator-prey interactions, foraging behaviour. Deacon et al. (2019) examine the effectiveness of the guppy as a biocontrol agent in India: control of

mosquito larvae being one of the main reasons for their introduction (Deacon et al. 2011). The authors show that when presented with two species of disease-spreading mosquito larvae (*Anopheles stephensi* and *Culex quinquefasciatus*), female guppies' prey preference depended on both the prevailing social and physical conditions. This is an important finding that has potential implications for the use of this species in mosquito control (Deacon et al. 2019). Camacho-Cervantes et al. (2019) investigate foraging in a native Mexican species, the twoline skiffia, *Skiffia bilineata*, that may coexist with invasive guppy populations. The authors found that twoline skiffia foraging efficiency is reduced when shoaling with either guppies, or with another invasive fish, the twospot livebearer, *Pseudoxiphophorus bimaculatus*, and present evidence that the fitness of the endangered native species may be decreased by the invasive species (Camacho-Cervantes et al. 2019).

The final poeciliid paper (Magellan et al. 2019) and the second of our contributions on invertebrate behaviour (Cerato et al. 2019) both look to the future of biological invasions in the context of potential climate change. Magellan et al. (2019) show that warm-acclimated mosquitofish from a Hong Kong population generally outperformed cool-acclimated fish in learning and exploratory tasks. Together with their behavioural flexibility, wide temperature tolerance and rapid learning ability, this may contribute to mosquitofishes' invasion success. Cerato et al. (2019), examine a native-invasive crayfish pair in Australia. They demonstrate that although the native *Euastacus spinifer* out-competed the invasive *Cherax destructor* at lower temperatures, just a 4 °C increase in temperature induced a competitive reversal and resulted in much higher combat-related mortality in the native crayfish (Cerato et al. 2019). Both sets of authors agree that predicted future temperature increases are likely to favour aquatic invasive species.

Our final research paper, by Myles-Gonzalez et al. (2019), epitomises one of the core principles of this Special Issue – that understanding of behaviour can aid management of aquatic invasive species. The authors examine how consistency in behaviour can influence the likelihood of trapping invasive sea lamprey, *Petromyzon marinus*, in the Great Lakes. Although lampreys do exhibit consistent behaviour types, this did not relate to migratory timing or trap capture rate. Nonetheless, the authors emphasize how knowledge of individual differences in behaviour can inform management by allowing more accurate population size estimates and targeted trapping of behavioural types (Myles-Gonzalez et al. 2019).

We finish this Special Issue with a book review. Sol and Weis (2019) draw on their recent edited book, *Biological Invasions and Animal Behaviour*, to highlight behavioural aspects of aquatic invasions. One of their main conclusions is that general rules are rare, as behaviour can be highly context dependent. However, two generalizations are apparent: first, that behavioural plasticity has a central role in the success of invasive

species, and second, that behaviour is intricately linked to life history. Aquatic ecologists have contributed to developing this research, but work is restricted to a few species and several fields of research are currently neglected. We join with the authors in their belief that “aquatic animals can continue ... to improve our understanding of the role of behaviour in biological invasions” (Sol and Weis 2019).

So how has the field of behaviour and invasions progressed in the last 20 years? We have presented here some of the many and varied ways in which behaviour is important in aquatic invasions, which represents two major changes. First, Holway and Suarez (1999) highlight competitive and aggressive interactions between invasive and native species as a key factor in invasion success. While this is clearly important, only one paper in this special issue focuses on competitive interactions (Cerato et al. 2019), while the rest focus on other behaviours, indicating that this field has expanded considerably in breadth in recent years. Indeed, predator-prey interactions emerge as the main behavioural focus of this special issue, a finding in agreement with Sol and Weis’s (2019) analysis. Second, Holway and Suarez (1999) focus almost exclusively on terrestrial examples, which may in part reflect the authors’ interests, but was also likely influenced by the available research. The papers in this Special Issue, which use fish, amphibian and invertebrate models, demonstrate that aquatic species can and do provide abundant information on the role of behaviour in biological invasions. Other changes are also evident. Holway and Suarez (1999) point out that the role of behaviour changes at different stages of the invasion process, but suggest that findings can be generalized between species and ecosystems. While elucidation of common factors in invasion success is the focus of extensive ongoing research, as Sol and Weis (2019) indicate generalizations are rare, and the role of behaviour is highly context dependent. A final advancement that is apparent from this Special Issue, as highlighted by several of the authors, is the increased focus on applying scientific research to the management of biological invasions. Although biological invasions in aquatic ecosystems offer a rich source of data for investigating behaviour, the main point of our work must be mediating the ongoing impacts of invasive species which can best be achieved through cooperation between all stakeholders. We urge invasion scientists to place more emphasis on the behaviour of their study species as this will reveal fascinating and, more importantly, useful contributions to our understanding of aquatic invasions and their potential management.

Despite the progress highlighted here, behaviour is still rarely considered in conservation (Berger-Tal et al. 2015). For anyone wishing to know more about behaviour and invasions, the Invasivesnet researcher profile list contains several behavioural experts (<https://www.invasivesnet.org>). The Animal Behaviour in Conservation Working Group of the Society for Conservation Biology provides a similar list of behaviour and conservation experts

(<https://conbio.org/groups/working-groups/animal-behavior-in-conservation-working-group>). More general information on animal behaviour can be found in the webpages of the Association for the Study of Animal Behaviour (UK: <https://www.asab.org>), the Animal Behavior Society (US: www.animalbehaviorsociety.org), and the Australian Association for the Study of Animal Behaviour (<https://www.assab.org>). Finally, we hope you find this Behaviour and Invasions Special Issue to be useful and enjoyable.

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