Current Zoology 60 (3): 417–427, 2014

Animal personality and the ecological impacts of freshwater non-native species

Tristan JUETTE[1, 2], Julien CUCHEROUSSET[1, 2], Julien COTE[1, 2*]

[1] CNRS, Université Paul Sabatier, ENFA; UMR 5174 EDB (Laboratoire Évolution & Diversité Biologique); 118 route de Narbonne, F-31062 Toulouse, France

[2] Université Toulouse 3 Paul Sabatier, CNRS; UMR5174 EDB, F-31062 Toulouse, France

Abstract While the ecological impacts of invasive species have been demonstrated for many taxonomic groups, the potential effects of behavioural variation among non-native individuals (i.e. personality) on these impacts have been largely overlooked. This is despite the fact that recent studies have demonstrated that, by nature, the three first stages of biological invasions (i.e. transport, establishment and spread) can lead to personality-biased populations. Freshwater ecosystems provide a unique opportunity to investigate this issue, notably because the ecological impacts of non-native species have been extensively documented and because animal personality has been widely studied using freshwater model species such as fishes. Here, we aim at developing some perspectives on the potential effects of animal personality on the ecological impacts of freshwater non-native species across levels of biological organizations. At the individual level, personality types have been demonstrated to affect the physiology, metabolism, life history traits and fitness of individuals. We used these effects to discuss how they could subsequently impact invaded populations and, in turn, recipient communities. We also discussed how these might translate into changes in the structure of food webs and the functioning of invaded ecosystems. Finally we discussed how these perspectives could interact with the management of invasive species [*Current Zoology* 60 (3): 417–427, 2014].

Keywords Biological invasions, Behavioural syndromes, Aquatic ecosystems, Temperaments, Behavioural types, Cascading effects

1 Introduction

Biological invasions, whereby a species is transported and introduced (intentionally or accidentally) beyond its native range, spreads and establishes self-sustained populations into new habitats, are increasingly occurring worldwide. Many studies have demonstrated that biological invasions induce important negative impacts on native biota across levels of biological organisations ranging from genes to ecosystems (e.g. Cucherousset and Olden, 2011; Mack et al., 2000; Ruiz et al., 1997). During the last two decades, most investi-gations in biological invasions have principally focused on determining the biological and ecological characteristics of non-native species underlying their invasiveness and their ecological impacts (Facon et al., 2006; Gurevitch et al., 2011,). For instance, studies have revealed that non-native have higher dispersal rate, disperse over longer distance or display higher reproductive rates than native species (Kolar and Lodge, 2001; Lodge, 1993; Moyle and Marchetti, 2006).

In the meantime, the ecological importance of intraspecific variations has been emphasised (Bolnick et al., 2011; Bolnick et al., 2003) but only a limited number of studies have started to focus on within-species variation in biological invasions (e.g. Cote et al., 2010; Cucherousset et al., 2012; Duckworth and Badyaev, 2007). Indeed, individuals vary in their phenotypic characteristics and life history traits, and these variations could confer differential abilities to invade and impact native biota. An important facet of intraspecific variations is animal personality, i.e. individual differences in behaviours (e.g. boldness, aggressiveness, activity, sociability, exploration) that are partially consistent across time and contexts (Reale et al., 2010; Sih et al., 2004). Personality types are related to life-history traits (e.g. dispersal, growth and reproduction) and can strongly influence the entire sequence of a biological invasion through effects at each stage. Although several studies have investigated the composition in personality types at the invasion front (e.g. Duckworth and Badyaev, 2007; Groen et al., 2012; Lopez et al., 2012), no study has yet discussed their potential effects on the ecological impacts of non-native species.

Received Feb. 17, 2014; accepted June 19, 2014.

∗ Corresponding author. E-mail: julien.cote@univ-tlse3.fr

Here, we first reviewed evidences of personality-biased processes occurring during the initial stages of biological invasions: transport and introduction, establishment and spread. We then discussed how these personality-biased stages can modify invasive success and invasiveness. We then developed a framework to understand the potential effects of animal personalities on the impacts of non-native species at the population, community and ecosystem levels. We finally discussed how this might interact with the management of invasive species. In this review, we developed our perspectives using freshwater ecosystems and organisms as models because many studies on animal personalities have been performed on freshwater organisms such as fishes (Conrad et al., 2011) and because freshwater ecosystems have been widely impacted by global changes, including biological invasions (Strayer, 2010). Fish are amongst the most widely introduced organisms in fresh waters where they induce ecological impacts across levels of biological organisation (CucheroussetJ and Olden, 2011).

2 Personality-biased Invasion

Invaders, i.e. those individuals settling out of their native range, represent a non-random subset of their populations (Carere and Gherardi, 2013; Chapple et al., 2012; Cote, 2010; Sih et al., 2012) with a particular array of phenotypic characteristics and life history traits that might, to some extent, be associated with personality type. Here, we synthesized how the three first stages of biological invasions (i.e. transport, establishment and spread; Lockwood et al., 2013) could lead to personality-biased non-native populations.

2.1 Personality-biased transport leading to first introduction

Transport followed by the intentional or accidental introduction of non-native organisms is the first step of biological invasion (Lockwood et al., 2013). Accidental introductions usually result from individuals entering human transportation as a by-product (e.g. ballast waters, fish consignments) that are released in a new environment (Davies et al., 2013; Wonham et al., 2000). Accidental introductions are not rare and represent, for instance, at least 8% of freshwater fish introductions (Gozlan, 2008). Chapple et al. (2012) extensively reviewed the bases of personality-biased transport and observed that boldness, activity and exploration (including neophobia) were often related to the tendency to approach human infrastructures. For example, bolder individuals were more likely to be found in urban environments (Evans et al., 2010), i.e. making them more likely to enter accidentally the transport stage. One of the first filters occurring during transport is the ability of individuals to survive, forage and find shelters in novel environments. Although bolder and more active/explorer individuals might find resources more easily during transportation, they should also be more easily detected during inspections (Chapple et al., 2012).

Personality types also play a major role in the intentional introductions of non-native species. Human have intentionally introduced a myriad of non-native freshwater species for sport fishing, fisheries, or biological controls (Lockwood et al., 2013; see Gozlan 2008 for freshwater fish). These intentional introductions often start by the capture of specimens in wild populations and animal capture in the wild is not a non-random process in regards to personality types as the probability of being captured varies with personality types (Biro and Dingemanse, 2009). For instance, the proportion of bolder/active rainbow trou *Oncorhynchus mykiss* (Walbaum, 1792) harvested was about three times higher than shy/inactive individuals (Biro and Post, 2008). In fresh waters, recreational anglers capture individuals with specific personality types, i.e. more aggressive or bolder (Sutter et al., 2012; Wilson et al., 2011) with the exception of one specific situation (Wilson et al., 2011). In some cases, these captured individuals can be used for stocking to create new and/or non-native populations.

2.2 Personality-biased establishment

Invaders face strong environmental pressures in their new environments and only those able to forage on novel items, to avoid novel predators, to resist to novel parasites and pathogens and to deal with new abiotic conditions can survive and establish self-sustained populations. Although behavioural flexibility can increase the ability of invaders to deal with novelty (Sol et al., 2008; Sol and Lefebvre, 2000; Sol et al., 2002), differences in personality types between invaders and non-invaders both between- and within-species have been reported. Besides differences in neophobia, behavioural plasticity or innovation (Martin and Fitzgerald, 2005; Pavlov et al., 2006; Sol and Lefebvre, 2000), non-native species, populations or individuals can display higher levels of aggression and foraging rates and outcompete their native counterparts (Chucholl et al., 2008; Groen et al., 2012; Pintor et al., 2008; Rehage et al., 2005a; Rehage et al., 2005b; Usio et al., 2001). For instance, several studies have demonstrated that invasive crayfish species can be more aggressive and superior competitors than the native crayfish species of the area they invaded (Chucholl et al., 2008; Usio et al., 2001), leading to differences in ecosystem-level processes such as litter breakdown (Dunoyer et al., 2014). Personality differences between introduced and native populations (Pintor and Sih, 2009; Pintor et al., 2008) could be caused by personality-biased introductions (see Section 2.1) and/or by personality-dependant selection during the establishment stage.

2.3 Personality-biased spread

Following establishment, non-native individuals might spread and this spread can be human-mediated. In these cases, human-mediated dispersers may display similar personality types than during transport (see Section 2.1). In other cases, the spread is natural and non-native species are characterized by a higher disper-sal propensity than native species (e.g. Bubb et al., 2006; Johnson and Carlton, 1996; Rehage and Sih, 2004; Wilson et al., 2004), which is often associated with the phenotypic differences resulting from transport and establishment. This phenotype/dispersal association has also been observed within non-native species whereby individuals at the invasion front have phenotypic attributes fastening dispersal (reviewed in Clobert et al., 2009; Cote et al., 2010) such as dispersal behaviour. In many species, dispersal behaviour is related to personality traits (Cote et al., 2010), notably in freshwater fish species such as trinidad killifish *Rivulus hartii* (Boulenger, 1890), western mosquitofish *Gambusia affinis* (Baird & Girard, 1853) and southern leatherside chub *Lepidomeda aliciae* (Jordan & Gilbert, 1881) (Cote et al., 2010; Fraser et al., 2001, Rasmussen and Belk, 2012). Specifically, dispersers were bolder, more exploratory, more active, asocial or more aggressive than residents. In western mosquitofish, for instance, dispersal was faster for more asocial individuals (Cote et al., 2013; Cote et al., 2010) and dispersal rate was higher in populations with bolder and more asocial individuals (Cote et al., 2011). Consequently, bolder, aggressive or asocial types are predicted to be dominant at the invasion front (Cote et al., 2010; Duckworth and Badyaev, 2007). In other words, if transport, introduction and establishment were themselves not personality-biased, it is likely that individuals of a given personality types would better survive and spread, resulting in a biased composition at the invasion front.

Overall, and although this can slightly be context-dependent (Cote et al., 2013), we expect that non-native populations should have a higher proportion of bolder, more active, asocial or more aggressive individuals than populations in the native range. The intensity and the direction of this bias might, however, differ between intentional and accidental introductions. Bolder, more active, asocial or more aggressive individuals are predicted to dominate in accidental introduction while personality biases in intentional introductions likely depend upon capture methods. On one hand, anglers probably capture bolder and more active individuals leading to similar predictions than for accidental introductions. On the other hand, the capture of a large number of individuals would require appropriate methods (e.g. seine netting) that might select for group living (i.e. social) and shyer individuals. Although these personality types are associated with differences in foraging performances and survival rates, the consequences on the success of non-native populations and on the ecological impacts on recipient biota of these personality-biased populations remain underappreciated (Sih et al., 2012; Wolf and Weissing, 2012).

3 Personality-biased Invasion and Their Invasive Success

Personality traits are associated with several physiological and life-history traits, creating the so-called ‘pace-of-life syndromes’ (Reale et al., 2010) and, within a species, individuals can be ranked along a pace-of-life continuum ranging from slow to fast life styles. Slow life style individuals are predicted to be shy, thorough and slow explorers, less aggressive and more social. Fast life style individuals are predicted to be bold, superficial and fast explorers, more aggressive and asocial. These life styles are expected to be associated with specific demographic traits. For instance, slow life style individuals display a lower growth rate, a delayed reproduction and a longer life span than fast life style individuals (Chiba et al., 2007; Smith and Blumstein, 2008). Because introduced individuals are expected to be bolder, more exploratory, aggressive and asocial, they might also display a faster life style.

Hence, one can expect invaders to have higher foraging rate, to grow faster, to reproduce earlier but, in turn, to face higher predation rates and to have lower life expectancy. Several studies have demonstrated that bold, active and aggressive freshwater fishes such as three-spined stickleback *Gasterosteus aculeatus* (Linnaeus, 1758), and brown trout *Salmo trutta* (Linnaeus, 1758), have a competitive advantage, notably for food acquisition, compared to shy, less active and less aggressive individuals (Sundstrom et al., 2004; Ward et al., 2004), leading to higher resources consumption and growth rate (e.g. Metcalfe et al., 1995; Pottinger and Carrick, 2001).

For instance, bolder Atlantic silversides *Menidia menidia* (Linnaeus, 1766) displayed a higher growth rate and a higher fecundity than shyer individuals (Walsh et al., 2006). Other studies also predicted a higher reproductive success for bolder or more aggressive individuals (Ariyomo and Watt, 2012; Colléter and Brown, 2011, but see Wilson et al. 2010). In turn, however, individuals with a higher activity level, more exploratory and bolder are subjected to a higher predation pressure (Biro and Post, 2008; Biro et al., 2003) which could lead to lower longevity and survival rate (Biro et al., 2007) from a trade-off between growth/fecundity and sur-vival/longevity. Predation pressure is one of the main selection pressures acting on different personality traits (Bell and Sih, 2007; Brydges et al., 2008). In three-spined sticklebacks, Brydges et al. (2008) demonstrated that, in rivers, individuals from high-predation populations were less bold and active than individuals from low-predated populations. On the contrary, in ponds, individuals under a high predation pressure were bolder and more active than individuals facing low predation pressure (Brydges et al., 2008). Differences between rivers and ponds could result from a predation risk-dependent modulation of personality-biased dispersal in rivers (Cote et al., 2013) and/or differences in predator species composition and their foraging strategies (Brydges et al., 2008) that could produce different personality-biased survival (Sih et al., 2012).

If invasive individuals are bolder, more exploratory, aggressive or asocial, one can expect them to forage more, to grow faster, to reproduce more but also to survive less to predators and this has actually been observed empirically when comparing introduced and native species (foraging: Pintor and Sih, 2009; Rehage et al., 2005b, reproduction: Vila-Gispert et al., 2005, survival to predation: Carlsson et al., 2009). We therefore predict that these characteristics could reinforce, to some extends, invasion success at least during the first generations following their introduction and their impacts in invaded communities.

4 Personality-biased Invasions and Their Ecological Impacts

Personality-biased non-native populations may exhibit different biological and ecological features that could modify their biological interactions with novel competitors, prey or predators. These differences may play a crucial role in driving the intensity and the propagation of ecological impacts across levels of biological organisations (Table 1).

4.1 Consequences on invaded populations

Through an increased foraging and growth rates, native prey and competitor's populations should be strongly impacted by bolder or more aggressive compared invaders compared to unbiased populations. This is reinforced by prey naivety, i.e. the fact that native species from the newly invaded habitats (and therefore naive to non-native species) may exhibit ineffective antipredator responses to novel predators since having a lack evolutionary history with non-native predators (Kuehne and Olden, 2012; Sih et al., 2010). In addition, several studies have demonstrated that invasive species are better foragers than species native from areas they invaded. For instance, Rehage et al. (2005b) showed that invasive mosquitofish *Gambusia affinis* (Baird & Girard, 1853) and *Gambusia holbrooki* (Girard, 1859) consume more food and are better competitors than their congeneric species with low invasive potential (i.e. *Gambusia hispaniolea* and *Gambusia geiseri* Hubbs & Hubbs, 1957), leading to and may have consequently a higher impact on prey populations. Similar predictions could be made when comparing populations of a species between the native range and the invaded area. Individuals with a higher foraging should have stronger impacts on native prey and competitors (Table 1), as observed in birds (Duckworth, 2008; Duckworth and Badyaev, 2007), arthropods (Le Breton et al., 2003), crustaceans (Wilson et al., 2004) and fish (Lederer et al., 2006; Simon and Townsend, 2003). In largemouth bass, *Micropterus salmoides* (Lacepède, 1802), a non-native species which was introduced in many countries notably for angling (Cucherousset and Olden, 2011), more exploratory individuals had higher prey consumption rates than less exploratory individuals, but only for a specific prey species (Nannini et al., 2012). Specifically, more exploratory individuals consumed three times more mosquito larvae than less exploratory individuals while the consumption rate of prey fish was not related to exploration behaviour. Thus, in addition to a quantitative impact on prey biomass, the personality types of invaders can also have qualitative impacts on native prey community composition and competitor populations (Table 1). More generally, bolder, more exploratory or less neophobic individuals are expected to be more generalist in term of habitat use (Wilson et al., 1993) and diet (Sibbald et al., 2009; Wolf and Weissing, 2012). Similarly, asocial individuals might forage on a larger spatial scale and on more diverse resources than more social individuals (Sibbald and Hooper, 2004). Consequently,

Table 1 Potential ecological impacts of personality-biased non-native individuals on different levels of biological organization (population, community and ecosystem) in invaded areas compared to the native range

Personality bias at the invasion front	Effect of bias on invaders traits	Predicted impacts on populations	Predicted impacts on communities	Predicted impacts on ecosystems
Bolder, more asocial, aggressive, exploratory and/or active	Higher foraging rate and competitive abilities	Reduced abundance of prey abundance (*exploitation*) and competitors (*exclusion*)[1]	Depletion of the lower trophic levels (*change in trophic cascade intensity*) *or/and* Increased abundance in higher trophic levels[5]	Modification of ecosystem processes through cascading effects across le vels of biological organization[13], for examples:
Bolder, more exploratory and less neophobic	Larger dietary breadth	Decreased abundance of several prey species, instead of a strong reduction in one prey species[2] *and/or* Reduced availability of alternative prey for competitive species	Homogenization of lower trophic levels[6] *and/or* Change in food web structure[7] *and/or* Unbalanced community equilibrium[8]	- Decreased primary productivity or degradation of physical properties of habitats if invaders are primary consumers
Bolder, more exploratory and more active	More often out of refuges, larger home range or more risks taken	Increased abundance of predators [3]	Increased abundance at the higher trophic levels, change in food chain length[9] *and/or* Increased abundance of species at similar trophic level (less predation)[10] *and/or* More connected food webs[11]	- Increased litter decomposition if invaders are decomposers
Bolder, more asocial, aggressive, exploratory and/or active	Personality related differences in population structure (age/size/condition)	Modification of population dynamics[4]	Changes in community structure[12]	- Increased primary productivity and decreased litter decomposition if invaders are secondary consumers

[1] Simon and Townsend (2003) and Lederer et al. (2006) have demonstrated the impacts on non-native species on prey communities, and Nannini et al. (2012) have demonstrated that more exploratory individuals have higher foraging rates than less exploratory individuals. [2] Nannini et al. (2012) have demonstrated that more exploratory individuals have higher foraging rates only on specific prey species and several studies showed a different diet breadth of invasive and non-invasive species/individuals (e.g. Azuma 1992, Sea and Chesson 2002). [3] Tablado et al. (2010) have demonstrated that non-native species can be beneficial for predator species. [4, 5, 6, 7, 8, 9, 10] No empirical evidence known. [11] predicted by Moya-Laraño (2011) but not yet demonstrated. [12] Vila-Gisperd et al. (2005) and Ribeiro et al. (2008) have demonstrated that personality could change invaders characteristics, and Arim et al. (2010) have demonstrated that these characteristics could impact communities and food webs but existence of a link between invader personality and community and food web has not yet been demonstrated. [13] For instance, Crooks (2002), Vanderploeg et al. (2002) and Simon and Townsend (2003) have already demonstrated that invaders could impact ecosystem functioning but the potential implications of invaders personality is still hypothetical.

personality-biased invasion could modify the level of trophic specialisation and dietary breadth of non-native species. This is supported by the fact that the dietary breadth of invasive and non-invasive species/individuals can be different (Azuma, 1992; Shea and Chesson, 2002 but see Rehage et al., 2005b).

Fast life style individuals have a higher exposure and vulnerability to predation by native species (Bell and Sih, 2007; McGhee et al., 2013), which can, under the assumption of personality-biased invasion, positively affect predator populations in invaded habitats by increasing prey availability (e.g. Tablado et al., 2010; Twardochleb et al., 2012). This is in line with the biotic resistance hypothesis whereby native predators target preferentially the non-native (and naive) prey (Carlsson et al., 2009). For example, Twardochleb et al. (2012) showed that predation by signal crayfish *Pacifastacus leniusculus* (Dana, 1852) can restrict the probability of invasion by New Zealand mud snails *Potamopyrgus antipodarum* (Gray, 1843). However, this phenomenon is likely to be highly dependent of the ability of native predators to target novel non-native prey. While this is expected to decrease predation pressure on native prey (e.g. Rodriguez, 2006), it can also increase the population size of predators, leading to more complex interactive effects and predator/prey dynamics in invaded communities and food webs (Noonburg and Byers, 2005, Table 1).

4.2 Consequences on invaded communities and food webs

Recent studies have demonstrated that interindividual trait variations (e.g. body morphology or trophic specialization), driven by the interplay between genetic and environmental processes, had strong ecological and evolutionary consequences, notably on communities and food webs (Bolnick et al., 2011; Bolnick et al., 2003; Wolf and Weissing, 2012). For example, trophic specialization and morphological differences caused by adaptative radiation impacted prey community in experimental freshwater ecosystems (Harmon et al., 2009). Post et al. (2008) demonstrated that intraspecific variations in morphology could also affect trophic interactions within a food web (Post et al., 2008). In the meantime, other studies have demonstrated the impacts of non-native species on community structure (Duxbury et al., 2010; Sanders et al., 2003). To our knowledge, no study has yet investigated the ecological effects of animal personalities on communities and food webs. However, as discussed previously, empirical evidences on direct interspecific interactions (i.e. consumption, competition and predation) influenced by individual personality and the ecology of biological invasions suggest that such effects could exist.

For instance, we believe that 'fast life style' non-native organisms can have complex and interactive effects on native prey communities and on the dynamic of food webs through effects on predator populations (Table 1). Bolder/active/aggressive invaders could out-compete native competitors and deplete lower trophic levels, but could, in turn, have positive effects on native predators and this might, directly or indirectly, modify the community structure of native species. Theoretically, this should tone down the negative impacts of invasion, but the higher population growth of native predators can also have negative effects on other native species (Noonburg and Byers, 2005; Tablado et al., 2010). The overall effects of invasion on native communities will therefore be highly context-dependent, depending on the relative vulnerabilities of non-native and native prey species and predators' abilities/preferences to capture non-native prey. Because vulnerability to predation and predator ability is driven by personality, both prey and predator personality types will affect the complex dynamics of their interactions (McGhee et al., 2013; Pruitt et al., 2012). For example, Moya-Laraño (2011) suggested that bolder and highly active individuals are likely to encounter more predators and prey than shyer and less-active individuals and food webs with bolder individuals should be more connected than the food web of shyer individuals (Moya-Laraño, 2011, Table 1).

Personality-biased populations differ in their dynamics, i.e. growth and mortality rates, and because population age-structure and individual mass or size in non-native populations could differ compared to populations in the native range (Ribeiro et al., 2008; Vila-Gispert et al., 2005), this could be caused of personality-biased invasion. Yet, many studies have demonstrated that modifications in age/size/mass structure in a population could impact communities and food webs (Arim et al., 2010). In addition, foraging behaviour and diet can differ among conspecific individuals with different phenotypes (see Ward et al., 2006 for a review with freshwater fish). For instance, within a cohort of young-of-the-year northern pike *Esox lucius* (Linnaeus, 1758) individuals differ in their trophic position and timing of ontogenetic niche shifts and that these dietary variations were associated with differences in emigration behaviour from natal habitats (Cucherousset et al., 2013). Although this has not yet been directly demonstrated, we therefore believe that personality-biased non-native populations could modify prey communities and food web differently of personality-unbiased populations or populations in the native range (Table 1).

By modifying community structure (i.e. the abundance of species within a community) and food web architecture (i.e. trophic links between species), personality-biased non-native populations could then modify the distribution of functional traits within native community, including changes in adult body mass, basal metabolic rate or egg size (McGill et al., 2006). Such modifications caused by non-native species have already been observed in aquatic ecosystems (Baxter et al., 2004; Chapin et al., 1997; Simon and Townsend, 2003; Townsend, 2003) but this has never been done by incorporating individual personality as a causal mechanisms and we believe this is a promising avenue for future investigations.

4.3 Consequences on the functioning of invaded ecosystems

Since a bias in personality types could modify the biotic interactions between species, we believe that it could subsequently modify ecosystem functioning through, for instance, modifications in the intensity of cascading effects (Werner and Peacor, 2006). We could hypothesise that personality traits should act on some of these components through cascading effects across different levels of biological organization (Table 1). Indeed, on one hand, it has been demonstrated that differences among individuals could modify ecosystem functioning (Harmon et al., 2009). For instance, Rudolf and Rasmussen (2012) demonstrated that differences in the ontogenetic stages within a predatory species could modify ecosystem respiration and primary productivity (Rudolf and Rasmussen, 2012). On the other hand, non-native freshwater species can impact ecosystem processes such as biochemical cycles, primary production, or the fluxes of energy and organisms between ecosystems (review in Cucherousset and Olden, 2011). For instance, Simon and Townsend (2013) found that the introduction of brown trout *Salmo trutta* (Linnaeus, 1758) in New-Zealand modified the distribution of many invertebrates, leading to a modification of primary productivity while other studies demonstrated the impacts of non-native species on the fluxes of nutrients, on the physical properties of the habitat (e.g. light, water) and on litter decomposition, and this was especially the case of ecosystem engineers (Crooks, 2002; Simon and Townsend, 2003; Vanderploeg et al., 2002). To date, however, no study has explicitly tested the potential impact of intraspecific variation in behaviour and animal personality in non-native species on ecosystem functioning (Sih et al., 2012; Wolf and Weissing, 2012). We think that the avenue is promising and should be prioritized for future research to provide an integrative understanding of the ecological impacts of non-native species and, more generally, of the role of intraspecific variability in phenotypes on ecosystem functioning. For instance, experimental design testing for the effects of personality composition of non-native populations (e.g. aggressive, intermediate, mixed and not aggressive) on native populations, communities and ecosystems functioning should provide new insights into our theoretical and applied understanding of the ecological impacts of invasive species (Fig. 1).

5 Perspectives: The Potential Implications of Animal Personality for the Management of Invasive Species

Biological invasions are one of the most important threats for global biodiversity and induce high economical and ecological costs in many countries worldwide (Luque et al., 2014; Pimentel et al., 2001). As a consequence, management strategies have been established to limit the spread of non-native species and potentially, their ecological impacts (Britton et al., 2011; Simberloff et al., 2013). The first step is to prevent species introduction and, if the species is introduced, then early detections can avoid their establishment and subsequent spread. If a non-native species is established and has spread, management programs are usually based on eradication (Britton, 2011; Simberloff et al., 2013) or on control programmes. In all cases, however, management plans do not take into account the existence of interindividual variations within non-native populations such as behavioural syndromes that can potentially interact with and/or decrease the efficiency of management plans.

Indeed, the capture of specimens in wild population is a personality-biased process as individual probability of being captured, by trapping or hunting in particular, vary with their behavioural types (Biro and Dingemanse, 2009). Therefore, we can expect that eradication plans only capture specimens with particular behaviour, modifying (increasing or decreasing the biases depending on the species and the capture methods) the personality composition of managed non-native populations. Uusi-Heikkilä et al. (2008) have demonstrated that some phenotypes, such as personality type, can be counter-selected by human activities and, in non-native populations, we believe that this can result in a change of

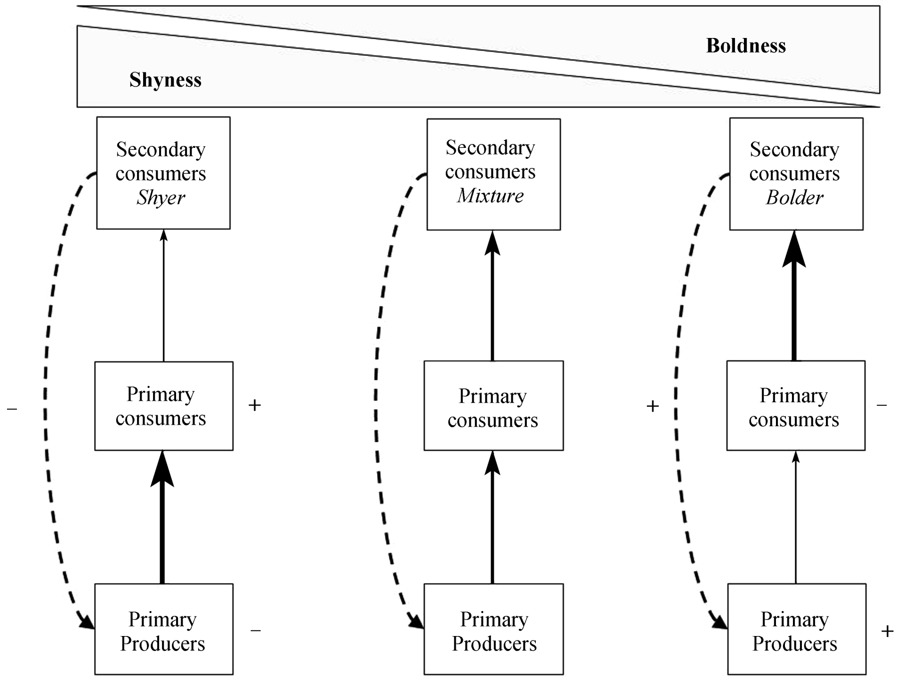

Fig. 1 Potential ecological effects driven by changes in personality composition (boldness/shyness) within a predator population (secondary consumer) in a simplified food web (three trophic levels: primary producers, primary consumers and secondary consumers)

Full and dotted arrows represent direct and indirect ecological effects, respectively.

population dynamic and potentially of food webs and ecosystem functioning (Uusi-Heikkilä et al., 2008). In some cases, this could annihilate the efficiency of management plans by modifying the ecological impacts of non-native species. Such effects of managements on the personality compositions are likely to occur at any stages of the invasions process. Therefore, we think that studies about the role of individual personality in non-native populations are also needed to improve the management of biological invasions (Reale et al., 2007; Wolf and Weissing, 2012). Finally, because our understanding of the genetic drivers of behavior is still scarce, we also believe that future investigations should appreciate the role of gene expression in driving individual personality and the genetically-biased characteristics of non-native populations to fully understand the interplay between ecological and evolutionary processes occurring through the invasion process.

Acknowledgements We are grateful to Elena Tricarico and three anonymous reviewers for their insightful comments on an earlier version of this manuscript. This work was supported by the Fondation FYSSEN and was done in EDB lab, part of the French Laboratory of Excellence project ‘‘TULIP” (ANR-10-LABX-41; ANR-11-IDEX-0002-02). JCu was supported by an ‘‘ERG Marie Curie’’ grant (PERG08-GA-2010-276969). JCo was supported by an ANR-12-JSV7-0004-01.

References

Arim M, Abades SR, Laufer G, Loureiro M, Marquet PA, 2010. Food web structure and body size: Trophic position and resource acquisition. Oikos 119: 147–153.

Ariyomo TO, Watt PJ, 2012. The effect of variation in boldness and aggressiveness on the reproductive success of zebrafish. Animal Behaviour 83: 41–46.

Azuma M, 1992. Ecological release in feeding behaviour: The case of bluegills in Japan. Hydrobiologia 243/244: 269–276.

Baxter CV, Fausch KD, Murakami M, Chapman PL, 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85: 2656–2663.

Bell AM, Sih A, 2007. Exposure to predation generates personality in threespined sticklebacks *Gasterosteus aculeatus*. Ecology Letters 10: 828–834.

Biro PA, Abrahams MV, Post JR, 2007. Direct manipulation of behaviour reveals a mechanism for variation in growth and mortality among prey populations. Animal Behaviour 73: 891–896.

Biro PA, Dingemanse NJ, 2009. Sampling bias resulting from animal personality. Trends in Ecology & Evolution 24: 66–67.

Biro PA, Post JR, 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proceedings of the National Academy of Sciences 105: 2919–2922.

Biro PA, Post JR, Parkinson EA, 2003. From individuals to populations: Prey fish risk-taking mediates mortality in whole-system experiments. Ecology 84: 2419–2431.

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM et al., 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26: 183–192.

Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM et al., 2003. The ecology of individuals: Incidence and implications of individual specialization. American Naturalist 161: 1–28.

Britton J, Gozlan RE, Copp GH, 2011. Managing non-native fish in the environment. Fish and Fisheries 12: 256–274.

Brydges NM, Colegrave N, Heathcote RJP, Braithwaite VA, 2008. Habitat stability and predation pressure affect temperament behaviours in populations of three-spined sticklebacks. Journal of Animal Ecology 77: 229–235.

Bubb DH, Thom TJ, Lucas MC, 2006. Movement, dispersal and refuge use of co-occurring introduced and native crayfish. Freshwater Biology 51: 1359–1368.

Carere C, Gherardi F, 2013. Animal personalities matter for biological invasions. Trends in Ecology & Evolution 28: 5–6.

Carlsson NOL, Sarnelle O, Strayer DL, 2009. Native predators and exotic prey: An acquired taste? Frontiers in Ecology and the Environment 7: 525–532.

Chapin FS, Walker BH, Hobbs RJ, Hooper DU, Lawton JH et al., 1997. Biotic control over the functioning of ecosystems. Science 277: 500–504.

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

Chiba S, Arnott S, Conover D, 2007. Coevolution of foraging behavior with intrinsic growth rate: Risk-taking in naturally and artificially selected growth genotypes of *Menidia menidia*. Oecologia 154: 237–246.

Chucholl C, Stich HB, Maier G, 2008. Aggressive interactions and competition for shelter between a recently introduced and an established invasive crayfish:*Orconectes immunis* vs.*O. limosus*. Fundamental and Applied Limnology / Archiv für Hydrobiologie 172: 27–36.

Clobert J, Le Galliard JF, Cote J, Meylan S, Massot M, 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12: 197–209.

Colléter M, Brown C, 2011. Personality traits predict hierarchy rank in male rainbowfish social groups. Animal Behaviour 81: 1231–1237.

Conrad JL, Weinersmith KL, Brodin T, Saltz JB, Sih A, 2011. Behavioural syndromes in fishes: A review with implications for ecology and fisheries management. Journal of Fish Biology 78: 395–435.

Cote J, Clobert J, Brodin T, Fogarty S, Sih A, 2010. Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. Philosophical Transactions of the Royal Society B: Biological Sciences 365: 4065–4076.

Cote J, Fogarty S, Brodin T, Weinersmith K, Sih A, 2011. Personality-dependent dispersal in the invasive mosquitofish: Group composition matters. Proceedings of the Royal Society B: Biological Sciences 278: 1670–1678.

Cote J, Fogarty S, Tymen B, Sih A, Brodin T, 2013. Personality-dependent dispersal cancelled under predation risk. Proceedings of the Royal Society B: Biological Sciences. doi: 10.1098/rspb.2013.2349.

Cote J, Fogarty S, Weinersmith K, Brodin T, Sih A, 2010. Personality traits and dispersal tendency in the invasive mosquitofish *Gambusia affinis.* Proceedings of the Royal Society B-Biological Sciences 277: 1571–1579.

Crooks JA, 2002. Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. Oikos 97: 153–166.

Cucherousset J, Olden JD, 2011. Ecological impacts of nonnative freshwater fishes. Fisheries 36: 215–230.

Cucherousset J, Bouletreau S, Martino A, Roussel JM, Santoul F, 2012. Using stable isotope analyses to determine the ecological effects of non-native fishes. Fisheries Management and Ecology 19: 111–119.

Cucherousset J, Paillisson J-M, Roussel J-M, 2013. Natal departure timing from spatially varying environments is dependent of individual ontogenetic status. Naturwissenschaften 100: 761–768.

Davies GD, Gozlan RE, Robert Britton J, 2013. Can accidental introductions of non-native species be prevented by fish stocking audits? Aquatic Conservation: Marine and Freshwater Ecosystems 23: 366–373.

Duckworth RA, 2008. Adaptive dispersal strategies and the dynamics of a range expansion. American Naturalist 172: S4–S17.

Duckworth RA, Badyaev AV, 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proceedings of the National Academy of Sciences of the United States of America 104: 15017–15022.

Dunoyer L, Dijoux L, Bollache L, Lagrue C, 2014. Effects of crayfish on leaf litter breakdown and shredder prey: Are native and introduced species functionally redundant? Biological Invasions 16: 1545–1555.

Duxbury C, Holland J, Pluchino M, 2010. Experimental evaluation of the impacts of the invasive catfish *Hoplostemum littorale* (Hancock, 1828) on aquatic macroinvertebrates. Aquatic Invasions 5: 97–102.

Evans J, Boudreau K, Hyman J, 2010. Behavioural syndromes in urban and rural populations of song sparrows. Ethology 116: 588–595.

Facon B, Genton BJ, Shykoff J, Jarne P, Estoup A et al., 2006. A general eco-evolutionary framework for understanding bioinvasions. Trends in Ecology & Evolution 21: 130–135.

Fraser DF, Gilliam JF, Daley MJ, Le AN, Skalski GT, 2001. Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. American Naturalist 158: 124–135.

Gozlan RE, 2008. Introduction of non-native freshwater fish: Is it all bad? Fish and Fisheries 9: 106–115.

Groen M, Sopinka NM, Marentett JR, Reddon AR, Brownscombe JW et al., 2012. Is there a role for aggression in round goby invasion fronts? Behaviour 149: 685–703.

Gurevitch J, Fox GA, Wardle GM, Inderjit, Taub D, 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. Ecology Letters 14: 407–418.

Harmon LJ, Matthews B, Des Roches S, Chase JM, Shurin JB et al., 2009. Evolutionary diversification in stickleback affects ecosystem functioning. Nature 458: 1167–1170.

Johnson LE, Carlton JT, 1996. Post-establishment spread in large-scale invasions: Dispersal mechanisms of the zebra *Mussel dreissena polymorpha*. Ecology 77: 1686–1690.

Kolar CS, Lodge DM, 2001. Progress in invasion biology: Pre-

dicting invaders. Trends in Ecology and Evolution 16: 199–204.
Kuehne LM, Olden JD, 2012. Prey naivety in the behavioural responses of juvenile Chinook salmon *Oncorhynchus tshawytscha* to an invasive predator. Freshwater Biology 57: 1126–1137.
Le Breton J, Chazeau J, Jourdan H, 2003. Immediate impacts of invasion by *Wasmannia auropunctata* (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest. Austral Ecology 28: 204–209.
Lederer A, Massart J, Janssen J, 2006. Impact of round gobies *Neogobius melanostomus* on Dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) and the associated macroinvertebrate community across an invasion front. Journal of Great Lakes Research 32: 1–10.
Lockwood JL, Hoopes MF, Marchetti MP, 2013. Invasion Ecology. Chicester: John Wiley & Sons.
Lodge DM, 1993. Biological invasions: Lessons for ecology. Trends in Ecology & Evolution 8: 133–137.
Lopez DP, Jungman AA, Rehage JS, 2012. Nonnative African jewelfish are more fit but not bolder at the invasion front: A trait comparison across an everglades range expansion. Biological Invasions 14: 2159–2174.
Luque GM, Bellard C, Bertelsmeier C, Bonnaud E, Genovesi P et al., 2014. The 100th of the world's worst invasive alien species. Biological Invasions 981–985.
Mack RN, Simberloff D, Mark Lonsdale W, Evans H, Clout M et al., 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10: 689–710.
Martin LB, Fitzgerald L, 2005. A taste for novelty in invading house sparrows *Passer domesticus*. Behavioral Ecology 16: 702–707.
McGhee KE, Pintor LM, Alison MB, 2013. Reciprocal behavioral plasticity and behavioral types during predator-prey interactions. The American Naturalist 182: 704–717.
Metcalfe NB, Taylor AC, Thorpe JE, 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. Animal Behaviour 49: 431–436.
Moya-Laraño J, 2011. Genetic variation, predator-prey interactions and food web structure. Philosophical Transactions of the Royal Society B: Biological Sciences. 366: 1425–1437.
Moyle PB, Marchetti MP, 2006. Predicting Invasion success: Freshwater fishes in California as a model. Bioscience 56: 515–524.
Nannini MA, Parkos J, Wahl DH, 2012. Do behavioral syndromes affect foraging strategy and risk-taking in a juvenile fish predator? Transactions of the American Fisheries Society 141: 26–33.
Noonburg EG, Byers JE, 2005. More harm than good: When invader vulnerability to predators enhances impact on native species. Ecology 86: 2555–2560.
Pavlov DS, Mikheev VN, Dgebuadze YY, 2006. Behavioral aspects of biological invasions of alien fish species. Journal of Ichthyology 46: S117–S124.
Pimentel D, McNair S, Janecka J, Wightman J, Simmonds C et al., 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agriculture, Ecosystems & Environment 84: 1–20.
Pintor L, Sih A, 2009. Differences in growth and foraging behavior of native and introduced populations of an invasive crayfish. Biological Invasions 11: 1895–1902.
Pintor LM, Sih A, Bauer ML, 2008. Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. Oikos 117: 1629–1636.
Post DM, Palkovacs EP, Schielke EG, Dodson SI, 2008. Intraspecific variation in a predator affects community structure and cascading trophic interactions. Ecology 89: 2019–2032.
Pottinger TG, Carrick TR, 2001. Stress responsiveness affects dominant-subordinate relationships in rainbow trout. Hormones and Behavior 40: 419–427.
Pruitt JN, Stachowicz JJ, Sih A, 2012. Behavioral types of predator and prey jointly determine prey survival: Potential implications for the maintenance of within-species behavioral variation. The American Naturalist 179: 217–227.
Rasmussen JE, Belk MC, 2012. Dispersal behavior correlates with personality of a North American fish. Current Zoology 58: 260–270.
Reale D, Dingemanse NJ, Kazem AJN, Wright J, 2010. Evolutionary and ecological approaches to the study of personality. Philosophical Transactions of the Royal Society B: Biological Sciences 365: 3937–3946.
Reale D, Garant D, Humphries MM, Bergeron P, Careau V et al., 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philosophical Transactions of the Royal Society B: Biological Sciences 365: 4051–4063.
Reale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ, 2007. Integrating animal temperament within ecology and evolution. Biological Reviews 82: 291–318.
Rehage JS, Barnett BK, Sih A, 2005a. Behavioral responses to a novel predator and competitor of invasive mosquitofish and their non-invasive relatives (*Gambusia* sp.). Behavioral Ecology and Sociobiology V57: 256–266.
Rehage JS, Barnett BK, Sih A, 2005b. Foraging behaviour and invasiveness: Do invasive *Gambusia* exhibit higher feeding rates and broader diets than their noninvasive relatives? Ecology of Freshwater Fish 14: 352–360.
Rehage JS, Sih A, 2004. Dispersal behavior, boldness, and the link to invasiveness: A comparison of four *Gambusia* species. Biological Invasions 6: 379–391.
Ribeiro F, Elvira B, Collares-Pereira M, Moyle P, 2008. Life-history traits of non-native fishes in Iberian watersheds across several invasion stages: A first approach. Biological Invasions 10: 89–102.
Rodriguez L, 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biological Invasions 8: 927–939.
Rudolf VHW, Rasmussen NL, 2012. Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem. Ecology 94: 1046–1056.
Ruiz GM, Carlton JT, Grosholz ED, Hines AH, 1997. Global Invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent, and consequences. American Zoologist 37: 621–632.
Sanders NJ, Gotelli NJ, Heller NE, Gordon DM, 2003. Community disassembly by an invasive species. Proceedings of the National Academy of Sciences 100: 2474–2477.
Shea K, Chesson P, 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution 17: 170–176.

Sibbald AM, Erhard HW, McLeod JE, Hooper RJ, 2009. Individual personality and the spatial distribution of groups of grazing animals: An example with sheep. Behavioural Processes 82: 319–326.

Sibbald AM, Hooper RJ, 2004. Sociability and the willingness of individual sheep to move away from their companions in order to graze. Applied Animal Behaviour Science 86: 51–62.

Sih A, Bell A, Johnson JC, 2004. Behavioral syndromes: An ecological and evolutionary overview. Trends in Ecology and Evolution 19: 372–377.

Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD et al., 2010. Predator-prey naivete, antipredator behavior, and the ecology of predator invasions. Oikos 119: 610–621.

Sih A, Cote J, Evans M, Fogarty S, Pruitt J, 2012. Ecological implications of behavioural syndromes. Ecology Letters 15: 278–289.

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA et al., 2013. Impacts of biological invasions: What's what and the way forward. Trends in Ecology & Evolution 28: 58–66.

Simon KS, Townsend CR, 2003. Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. Freshwater Biology 48: 982–994.

Smith BR, Blumstein DT, 2008. Fitness consequences of personality: A meta-analysis. Behav. Ecol. 19: 448–455.

Sol D, Bacher S, Simon MR, Lefebvre L, 2008. Brain size predicts the success of mammal species introduced into novel environments. The American Naturalist 172: S63–S71.

Sol D, Lefebvre L, 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. Oikos 90: 599–605.

Sol D, Timmermans S, Lefebvre L, 2002. Behavioural flexibility and invasion success in birds. Animal Behaviour 63: 495–502.

Strayer DL, 2010. Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55: 152–174.

Sundstrom LF, Petersson E, Hojesjo J, Johnsson JI, Jarvi T, 2004. Hatchery selection promotes boldness in newly hatched brown trout *Salmo trutta*: Implications for dominance. Behavioral Ecology 15: 192–198.

Sutter DAH, Suski CD, Philipp DP, Klefoth T, Wahl DH et al., 2012. Recreational fishing selectively captures individuals with the highest fitness potential. Proceedings of the National Academy of Sciences 109: 20960–20965.

Tablado Z, Tella JL, Sanchez-Zapata JA, Hiraldo F, 2010. The paradox of the long-term positive effects of a North American crayfish on a European community of predators. Conservation Biology. 24: 1230–1238.

Townsend CR, 2003. Individual, population, community, and ecosystem consequences of a fish invader in New Zealand Streams. Conservation Biology. 17: 38–47.

Twardochleb LA, Novak M, Moore JW, 2012. Using the functional response of a consumer to predict biotic resistance to invasive prey. Ecological Applications 22: 1162–1171.

Usio N, Konishi M, Nakano S, 2001. Species displacement between an introduced and a ‘vulnerable’ crayfish: The role of aggressive interactions and shelter competition. Biological Invasions 3: 179–185.

Uusi-Heikkilä S, Wolter C, Klefoth T, Arlinghaus R, 2008. A behavioral perspective on fishing-induced evolution. Trends in Ecology & Evolution 23: 419–421.

Vanderploeg HA, Nalepa TF, Jude DJ, Mills EL, Holeck KT et al., 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 59: 1209–1228.

Vila-Gispert A, Alcaraz C, García-Berthou E, 2005. Life-history traits of invasive fish in small Mediterranean streams. Biological Invasions 7: 107–116.

Ward A, Thomas P, Hart PJB, Krause J, 2004. Correlates of boldness in three-spined sticklebacks *Gasterosteus aculeatus*. Behavioral Ecology and Sociobiology 55: 561–568.

Ward AJW, Webster MM, Hart PJB, 2006. Intraspecific food competition in fishes. Fish and Fisheries 7: 231–261.

Werner EE, Peacor SD, 2006. Lethal and nonlethal predator effects on an herbivore guild mediated by system productivity. Ecology 87: 347–361.

Wilson ADM, Binder TR, McGrath KP, Cooke SJ, Godin J-GJ, 2011. Capture technique and fish personality: Angling targets timid bluegill sunfish *Lepomis macrochirus*. Canadian Journal of Fisheries and Aquatic Sciences 68: 749–757.

Wilson ADM, Godin J-GJ, Ward AJW, 2010. Boldness and reproductive fitness correlates in the eastern mosquitofish *Gambusia holbrooki*. Ethology. 116: 96–104.

Wilson DS, Coleman K, Clark AB, Biederman L, 1993. Shy-bold continuum in pumpkinseed sunfish *Lepomis gibbosus*: An ecological study of a psychological trait. Journal of Comparative Psychology 107: 250.

Wilson KA, Magnuson JJ, Lodge DM, Hill AM, Kratz TK et al., 2004. A long-term rusty crayfish *Orconectes rusticus* invasion: Dispersal patterns and community change in a north temperate lake. Canadian Journal of Fisheries and Aquatic Sciences 61: 2255–2266.

Wolf M, Weissing FJ, 2012. Animal personalities: Consequences for ecology and evolution. Trends in Ecology & Evolution 27: 452–461.

Wonham MJ, Carlton JT, Ruiz GM, Smith LD, 2000. Fish and ships: Relating dispersal frequency to success in biological invasions. Marine Biology 136: 1111–1121.