Current Zoology 61 (6): 966–971, 2015

Temperature increase impacts personality traits in aquatic non-native species: Implications for biological invasion under climate change

Dapeng ZHAO[1*], Peishan FENG

Tianjin Key Laboratory of Animal and Plant Resistance, College of Life Sciences, Tianjin Normal University, Tianjin 300387, China

Abstract Climate change, such as elevated temperatures, may facilitate biological invasion. Aquatic animal systems are more vulnerable to biological invasion when the temperature rises. Animal personality also plays an important role in the possibility of successful establishment of invasive species. However, it is still unclear how personality traits of invasive species will respond to global warming. This study focuses on juveniles of red swamp crawfish *Procambarus clarkii*, an invasive poikilothermic species with wide distribution throughout the world, and explores how slight temperature increases influence three personality traits (activity, boldness and aggressiveness) of *P. clarkii*. For each personality, individual variation is to be presented in condition of the same temperature. Individual personality values can significantly increase with the subtle rising of water temperature. Significant correlations among activity, boldness and aggressiveness are found at any temperature stage, and such relationships are maintained at a similar level in the face of different temperatures. It is most likely that significant expressions of personality traits may be an ecological compensation strategy to offset increased metabolic costs when faced with small temperature increases. Aggression syndromes are formed due to stable linkages between personality traits, in order to acquire allopatric resources efficiently and establish a new population in this species [*Current Zoology* 61 (6): 966–971, 2015].

Keywords Animal personality, Biological invasion, Climate change, Crawfish, Invasive species

The ongoing climate change is a formidable challenge for global organisms. Climate change is mainly reflected by the varying degrees of temperature, carbon dioxide levels and precipitation (Walther et al., 2002; Hughes et al., 2003). Climate change provide non-native species with the colonization opportunity during the biological invasion process (Hellmann et al., 2008; Rahel and Olden, 2008). The primary cause is that invasive species outperform native species in some areas of socioecological adaptations (e.g. higher dispersal tendencies, as well as rapid growth and reproductive rates), which may be conducive to effectively overcoming environmental challenges caused by climate change (Kolar and Lodge, 2001; Sorte et al., 2013). Native and invasive species, especially plants, perform similarly well when coping with climate changes in terrestrial systems (Sorte et al., 2013). By contrast, invasive species, especially animals (e.g. crawfishes), show better performances than native species in aquatic systems when temperature is elevated (Sorte et al., 2013). In other words, aquatic animal systems are more vulnerable to biological invasion when temperature rise occurs, and it deserves special attention with consideration for biological conservation (Rahel and Olden, 2008).

With regard to the topic of biological invasion, many previous studies tend to focus on the comparison of inter-specific behavioral and ecological characteristics during the invasion (Facon et al., 2006; Gurevitch et al., 2011). In the last decade, new research approaches on biological invasion have been increasingly emphasized, which pay close attention to ecological adaptation of intra-specific behavioral variation (i.e. animal personality) (Duckworth and Badyaev, 2007; Cote et al., 2010; Cote et al., 2011; Fogarty et al., 2011; Gherardi et al., 2012; Carvalho et al., 2013; Cote et al., 2013; Brodin and Drotz, 2014). As has been verified already, animal personalities (assessed for example through activity, boldness, aggressiveness) play an important role in the possibility of successful establishment of an invasive species (Rehage and Sih, 2004; Chapple et al., 2012; Carere and Gherardi, 2013; Juette et al., 2014). For instance, aggressiveness is considered a particularly important behavioral feature, which may help to predict whether the establishment of invasive species is suc-

Received Dec. 11, 2014; accepted Mar. 18, 2015.

* Corresponding author. E-mail: zdp_0609@163.com, skyzdp@mail.tjnu.edu.cn

cessful or not (Weis, 2010; Hudina et al., 2014). Furthermore, some personality traits could be integrated into the behavioral syndrome, so as to improve the success rate of invasion in different stages (including establishment, spreading, and integration) (Fogarty et al., 2011). Given that ecological change could affect individual fitness via animal personality (Réale et al., 2007), it is worth exploring how climate change impact personality traits of invasive aquatic species by means of experimental environmental simulation. However, it is still unclear how personality traits of invasive species will respond to climatic changes (e.g. elevated temperature).

The red swamp crawfish *Procambarus clarkii* is one invasive poikilothermic species with the widest distribution among all crustaceans. Its original location was in Southeastern U.S.A. and Mexico (Gherardi, 2006; Gherardi and Acquistapace, 2007; Gherardi et al., 2011; Hanshew and Garcia, 2012). Socioecological plasticity of *P. clarkii* and artificial transportation contributed to its rapid spread throughout the world (Gherardi, 2006). *P. clarkii* plays an important role in freshwater food webs (Correia, 2002; Geiger et al., 2005; Carreira et al., 2014). The main purposes of this paper are to investigate temporal stability of three personality traits (boldness, aggressiveness, and activity) of *P. clarkii* under the same temperature environment, and to explore how temperature increase influence personality traits of this invasive species. Considering that the crayfish belongs to ectothermic species, it is predicted that indications of these personality traits of this invasive species will increase along with temperature rise.

1 Materials and Methods

1.1 Study of species and experimental procedures

Red swamp crayfish were obtained from a commercial fish producer. Thirty juvenile individuals with near-equal body sizes (mean length = 35.5 mm, *SD* = 3.5) were selected as the test subjects. We used juveniles instead of adults being this stage important for species' invasion capability. We did not explore sex differences in that it is difficult to identify the sex for juvenile crayfishes. Before the start of experimental tests, each individual was raised separately for one day in an opaque plastic case (132 mm × 96 mm × 40 mm) under the room temperature and normal photoperiod so as to simulate a predator-free environment. Ceramic rings were placed inside as hiding sites for crayfishes. Individuals were acclimated to any temperature stage for one hour before testing.

The experiment consisted of two temperature stages, in which the lower water temperature (26 ± 0.2°C) at first and then the higher water temperature (29 ± 0.3°C) were maintained. We kept the same test order among individuals across two temperature stages when measuring each personality trait. Each individual at any temperature stage was tested twice a day, once in the morning (8:30 to 10:30 a.m.) and once in the afternoon (2:30 to 4:30 p.m.). The test interval was about 6 hours. The same experiment was then repeated for four continuous days for each individual at any temperature stage. Totally there were eight repeated tests for each personality trait of each individual under each temperature stage.

To measure boldness, we put a shrimp net in the center of the case so as to simulate the threat of being caught. As a result, crayfish responded by escaping to the ceramic rings. We estimated boldness with the latency for individuals getting away from the net into ceramic rings. The shorter the latency is, the higher boldness values are. To measure aggressiveness, we applied the classic mirror test. One small mirror was placed in the center of the case in order to simulate the existence of a newly introduced individual of the same species. Aggressiveness was evaluated by recording the frequency of rapid swimming by the crayfishes directly towards the mirror for a period of one minute. To measure activity, we recorded the accumulated moving time with active locomotion within three minutes for each individual. It included any movement that the individuals made.

Our research adhered to the Chinese Government's legal requirements concerning animal research. This study conforms to the provisions of the Declaration of Helsinki.

1.2 Data analysis

To assess personality traits at different temperatures, the general linear mixed model was adopted (Biro et al., 2010; Briffa et al., 2013) and the personality values were ln (x + 1) transformed prior to the analysis for the purpose of data normalization. A model was built based on the methods described by Biro et al. (2010) and Briffa et al. (2013). Ambient temperature was specified as the main fixed effect, and the intercept and slope of the personality traits, along with temperature changes, were taken as random effects in the final model. Furthermore, the covariance structure type was set as "unstructured". The random intercept effect displayed the contextual generality while the random slope effect displayed the contextual plasticity (Biro et al., 2010;

Dingemanse et al., 2010; Stamps and Groothuis, 2010). The contextual generality suggests whether the individual who had higher behavioral scores than others at one temperature stage also display higher scores at another temperature stage. The contextual plasticity suggests whether some individuals have stronger behavioral responses to temperature increase than others (Biro et al., 2010). Test orders and test days were considered as covariates.

To examine relationships between personality traits, the model-calculated predicted values for each individual, at the lower and higher temperature stages, respectively, were achieved with the application of Spearman correlations test, and all of the analyses were conducted with SPSS 21.0.

2 Results

2.1 Temperature impacts

With regard to activity, individual values increased significantly along with a small rise in water temperature (F = 38.485, P < 0.001; Fig. 1). Individual activities did not show significant contextual generality (random intercept effect: Z = 1.633, P = 0.102) and contextual plasticity (random slope effect: Z = 0.887, P = 0.375) as the temperature varied. Based on normalized values, 26 individuals showed an increase in activity, but a slight decrease was suggested for the remaining 4 individuals (Fig. 1). Additionally, activity was significantly changed over the test orders (F = 7.064, P < 0.001) and test days (F = 19.185, P < 0.001).

As for aggressiveness, individual values showed a significant increase along with small temperature increases (F = 4.214, P = 0.050; Fig. 2). Individuals generally did not show significant contextual generality (random intercept effect: Z = 1.856, P = 0.064) or contextual plasticity (random slope effect: Z = 1.601, P = 0.109) as the temperature changed. 24 individuals increased their aggressiveness and a decrease was evident for the remaining 6 individuals based on normalized values (Fig. 2). Moreover, individual aggressiveness did not change significantly over the test days (F = 3.174, P = 0.075) as compared to test orders (F = 13.601, P < 0.001).

In terms of boldness, individual values decreased significantly along with a small rise in temperature (F = 25.097, P < 0.001; Fig. 3). Individuals generally did not show significant contextual generality (random intercept effect: Z = 1.367, P = 0.172) or contextual plasticity (random slope effect: Z = 0.928, P = 0.354) as the

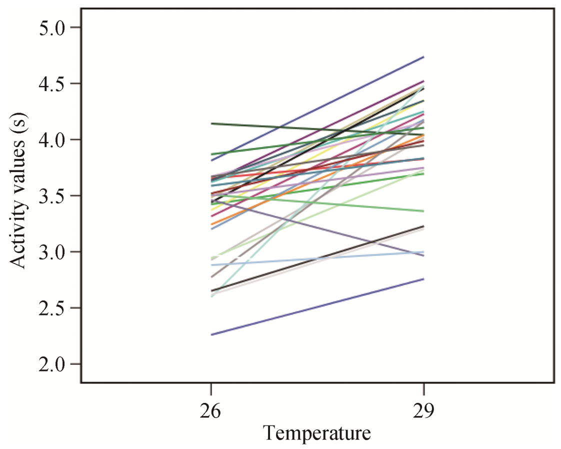

Fig. 1 Activity levels across temperature rise with normalized data

Average values were shown for test individuals at each temperature stage.

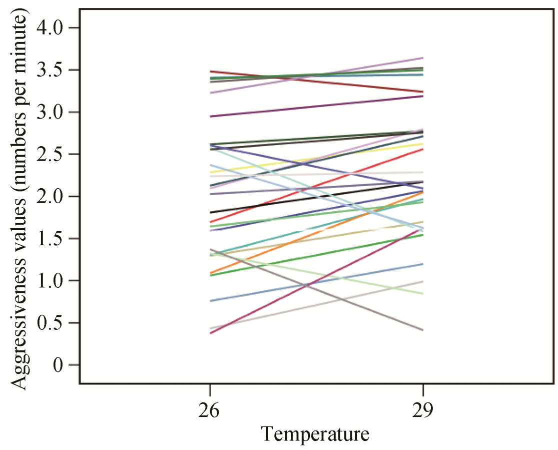

Fig. 2 Aggressiveness levels across temperature rise with normalized data

Average values were shown for test individuals at each temperature stage.

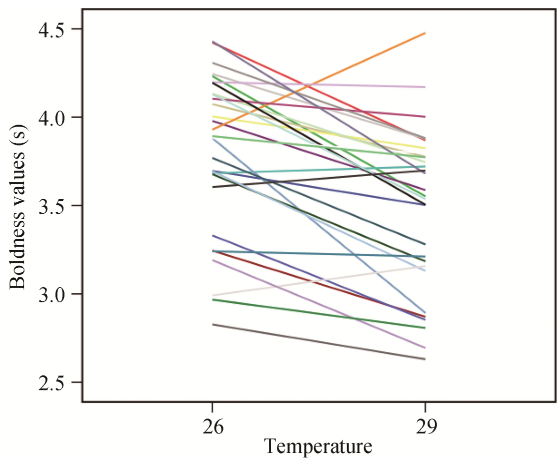

Fig. 3 Boldness levels across temperature rise with normalized data

Average values were shown for test individuals at each temperature stage.

temperature changed. 26 individuals increased their boldness and a decrease was suggested for the remaining 4 individuals based on normalized values (Fig. 3). Individual boldness did not change significantly over test days (F = 0.171, P = 0.679) as compared to test orders (F = 19.200, P < 0.001).

2.2 Relationship of personality traits

Through the observation of individuals at different temperatures, we found that: 1) activity was positively correlated with aggressiveness (26°C: r = 0.881, P < 0.001; 29°C: r = 0.881, P < 0.001); 2) boldness was negatively correlated with activity (26°C: r = -0.524, P < 0.001; 29°C: r = -0.524, P < 0.001); and 3) there was no significant correlation between aggressiveness and boldness (26°C: r = -0.071, P = 0.270; 29°C: r = -0.071, P = 0.270).

3 Discussion

To the best of our knowledge, we present the first investigation on the personality traits and temporal stability of juvenile red swamp crawfishes *Procambarus clarkii*, as well as the first examination on how temperature change impacts personality traits of this invasive crayfish species. As each red swamp crawfish was cultivated separately in their own shrimp box, observed individual behavioral differences cannot be reflected by different cultivation environment, which indicates the change in personality traits was most likely influenced by elevated water temperatures. It should be noted that the isolated cultivation environment may influence the expression of crayfish behavior (e.g. Drozdz et al., 2006; Hanshew and Garcia, 2012).

Personality traits have been found in aquatic animal species (Magnhagen, 2012; Rasmussen and Belk, 2012; Stein and Bell, 2012). For red swamp crawfishes, individual variation was obvious for each personality trait at the same temperature stage. For instance, some individuals showed more than sevenfold mean values of aggressiveness than others. Such intra-specific personality polymorphism is crucial for invasive species during biological invasion in that the integration of personality traits with different degrees could contribute to quicker and higher invasion throughout all three stages of biological invasion (Fogarty et al., 2011; Sih et al., 2012).

Personality traits may change throughout individual development process prior to sexual maturity (Stamps and Groothuis, 2010; Menzies et al., 2013). Personality values may significantly change over test orders and individuals did not show significant contextual generality and contextual plasticity in each personality test, which suggests that personality traits are temporally unstable at this given young age, as indicated by *P. clarkii*. However, individual aggressiveness and boldness did not significantly change over test days, which to some extent suggest that boldness and aggressiveness can be considered as predetermined personality traits in *P. clarkii*.

Temperature is one important factor influencing animal behavior, especially for ectothermic species (Biro et al., 2010; Vainikka et al., 2011; Pruitt et al., 2011; Gherardi et al., 2012; Briffa et al., 2013; Frost et al., 2013). As expected, *P. clarkii* displayed mean-values of personality traits that increased along with the elevated temperature, which is consistent with other ectothermic species (e.g. *Pomacentrus moluccensis*: Biro et al., 2010; *Anelosimus studiosus*: Pruitt et al., 2011). The potential reasons could be explained in two steps. First, temperature displays a multiplicative influence on metabolic rates in ectotherms, and even small temperature changes will cause significant increases in metabolic rate (Clarke and Johnston, 1999). Second, increasing metabolic rates generally result in the consumption of more energy costs and higher rates of food intake, so as to maintain stable individual growth rates (Schmidt-Nielsen, 1997). Correspondingly, significantly increased activity, aggressiveness and boldness of *P. clarkii* could improve foraging frequency and efficiency of species dramatically, in order to compensate for increased metabolic costs (Biro et al., 2010; Pruitt et al., 2011; Carere and Gherardi, 2013). It is most likely that significant expressions of personality traits may be an ecological compensation strategy when facing small temperature increases, at least for this invasive aquatic species.

Correlations between personality traits reflect inter-individual consistency in a wide range of environmental situations with important ecological and evolutionary implications (Sih et al., 2004; Réale et al., 2007). Positive correlations between aggressiveness, boldness, activity, and dispersal tendency could improve positive correlations of the three stages (establishment, spreading and integration of biological invasion) during the biological invasion (Sih et al., 2012). For *P. clarkii*, significant correlations between activity, boldness and aggressiveness were found at each temperature stage, which is consistent with related findings in other invasive species (e.g. *Pacifastacus leniusculus*: Pintor et al., 2008). Furthermore, such consistent relationships remain at similar levels in various temperature stages, which are in accordance with previous studies for other ectotherms (e.g. *Pomacentrus moluccensis*: Biro et al., 2010). These consistent relationships among personality traits may be driven by individual difference for metabolic rates, which are found to be stable over time in a variety of animal taxa (Nespolo and Franco, 2007). Stable linkages of personality traits could lead to the formation of aggression syndromes (Pintor et al., 2008), which may help for efficiently acquiring allopatric resources and establishing new populations in red swamp crawfishes.

On the whole, we found that red swamp crawfishes displayed significantly higher values for three personality traits in the face of small temperature increases. The pronounced reactions suggest that *P. clarkii* owns potential behavioral flexibility to adapt to its ecology and life cycle along with climate change. However, the present study should be treated with caution due to the use of captive bred individuals, the potential sex difference, as well as the availability of only one indicator corresponding to climate change. Further investigations are recommended to explore the impact of multiple indices (e.g. temperature, carbon dioxide content, and oxygen content) of climate change on personality traits of wild-caught individuals, so as to provide the general framework on ecological adaptation to climate change by wild invasive species (Brommer, 2013).

Acknowledgements This study was funded by Talent Introduction Fund of Tianjin Normal University of China (No. 5RL115) and “More Than One Thousand Talents Introduction within Three Years” Fund of Tianjin City of China (No. 5KQM110002). The authors have no conflict of interests in this research.

References

Biro PA, Beckmann C, Stamps JA, 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. Pro. R. Soc. Lond. B. 277: 71–77.

Briffa M, Bridger D, Biro PA, 2013. How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. Anim. Behav. 86: 47–54.

Brodin T, Drotz MK, 2014. Individual variation in dispersal associated behavioral traits of the invasive Chinese mitten crab (*Eriocheir sinensis*, H. Milne Edwards, 1854) during initial invasion of Lake Vänern, Sweden. Curr. Zool. 60: 410–416.

Brommer JE, 2013. Phenotypic plasticity of labile traits in the wild. Curr. Zool. 59: 485–505.

Carere C, Gherardi F, 2013. Animal personalities matter for biological invasions. Trends Ecol. Evol. 28: 5–6.

Carreira BM, Dias MP, Rebelo R, 2014. How consumption and fragmentation of macrophytes by the invasive crayfish *Procambarus clarkii* shape the macrophyte communities of temporary ponds. Hydrobiologia 721: 89–98.

Carvalho CF, Leitao AV, Funghi C, Batalha HR, Reis S et al., 2013. Personality traits are related to ecology across a biological invasion. Behav. Ecol. 24: 1081–1091.

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

Clarke A, Johnston N, 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. J. Anim. Ecol. 68: 893–905.

Correia AM, 2002. Niche breadth and trophic diversity: Feeding behaviour of the red swamp crayfish *Procambarus clarkii* towards environmental availability of aquatic macroinvertebrates in a rice field (Portugal). Acta Oecol. 23: 421–429.

Cote J, Fogarty S, Brodin T, Weinersmith K, Sih A, 2011. Personality-dependent dispersal in the invasive mosquitofish: Group composition matters. Proc. R. Soc. Lond. B. 278: 1670–1678.

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

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

Dingemanse NJ, Kazem AJ, Réale D, Wright J, 2010. Behavioural reaction norms: Animal personality meets individual plasticity. Trends Ecol. Evol. 25: 81–89.

Drozdz JK, Viscek J, Brudzynski SM, Mercier AJ, 2006. Behavioral responses of crayfish to a reflective environment. J. Crustacean Biol. 26: 463–473.

Duckworth RA, Badyaev AV, 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proc. Natl. Acad. Sci. 104: 15017–15022.

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

Fogarty S, Cote J, Sih A, 2011. Social personality polymorphism and the spread of invasive species: A model. Am. Nat. 177: 273–287.

Frost AJ, Thomson JS, Smith C, Burton HC, Davis B et al., 2013. Environmental change alters personality in the rainbow trout *Oncorhynchus mykiss*. Anim. Behav. 85: 1199–1207.

Geiger W, Alcorlo P, Baltanas A, Montes C, 2005. Impact of an introduced Crustacean on the trophic webs of Mediterranean wetlands. Biol. Invasions 7: 49–73.

Gherardi F, 2006. Crayfish invading Europe: The case study of *Procambarus clarkii*. Mari. Freshw. Behav. Phy. 39: 175–191.

Gherardi F, Acquistapace P, 2007. Invasive crayfish in Europe: The impact of *Procambarus clarkii* on the littoral community of a Mediterranean lake. Freshwater Biol. 52: 1249–1259.

Gherardi F, Aquiloni L, Diéguez-Uribeondo J, Tricarico E, 2011. Managing invasive crayfish: Is there a hope? Aquat. Sci. 73: 185–200.

Gherardi F, Aquiloni L, Tricarico E, 2012. Behavioral plasticity, behavioral syndromes and animal personality in crustacean decapods: An imperfect map is better than no map. Curr. Zool. 58: 567–579.

Gurevitch J, Fox G, Wardle G, Taub D, 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. Ecol. Lett. 14: 407–418.

Hanshew BA, Garcia TS, 2012. Invasion of the shelter snatchers: Behavioural plasticity in invasive red swamp crayfish *Pro-*

cambarus clarkii. Freshwater Biol. 57: 2285–2296.

Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS, 2008. Five potential consequences of climate change for invasive species. Conserv. Biol. 22: 534–543.

Hudina S, Hock K, Žganec K, 2014. The role of aggression in range expansion and biological invasions. Curr. Zool. 60: 401–409.

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR et al., 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301: 929–933.

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

Kolar CS, Lodge DM, 2001. Progress in invasion biology: Predicting invaders. Trends Ecol. Evol. 16: 199–204.

Magnhagen C, 2012. Personalities in a crowd: What shapes the behaviour of Eurasian perch and other shoaling fishes? Curr. Zool. 58: 35–44.

Menzies AK, Timonin ME, McGuire LP, Willis CK, 2013. Personality variation in little brown bats. PLoS ONE 8: e80230.

Nespolo RF, Franco M, 2007. Whole-animal metabolic rate is a repeatable trait: A meta-analysis. J. Exp. Biol. 210: 2000–2005.

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.

Pruitt JN, Demes KW, Dittrich-Reed DR, 2011. Temperature mediates shifts in individual aggressiveness, activity level, and social behavior in a spider. Ethology 117: 318–325.

Rasmussen JE, Belk MC, 2012. Dispersal behavior correlates with personality of a North American fish. Curr. Zool. 58: 260–270.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ, 2007. Integrating animal temperament within ecology and evolution. Biol.Rev. 82: 291–318.

Rahel FJ, Olden JD, 2008. Assessing the effects of climate change on aquatic invasive species. Conserv. Biol. 22: 521–533.

Rehage JS, Sih A, 2004. Dispersal behavior, boldness, and the link to invasiveness: A comparison of four *Gambusia* species. Biol. Invasions 6: 379–391.

Schmidt-Nielsen K, 1997. Animal Physiology: Adaptation and Environment. Cambridge: Cambridge University Press.

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

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

Sorte CJB, Ibáñez I, Blumenthal DM, Molinari NA, Miller LP et al., 2013. Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecol. Lett. 16: 261–270.

Stamps J, Groothuis TG, 2010. The development of animal personality: Relevance, concepts and perspectives. Biol. Rev. 85: 301–325.

Stein LR, Bell AM, 2012. Consistent individual differenes in fathering in threespined stickleback *Gasterosteus aculeatus*. Curr. Zool. 58: 45–52.

Vainikka A, Rantala MJ, Niemelä P, Hirvonen H, Kortet R, 2011. Boldness as a consistent personality trait in the noble crayfish *Astacus astacus*. Acta Ethol. 14: 17–25.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C et al., 2002. Ecological responses to recent climate change. Nature 416: 389–395.

Weis JS, 2010. The role of behavior in the success of invasive crustaceans. Mar. Freshw. Behav. Phy. 43: 83–98.