Bringing animal personality research into the food web arena

The consumption rate of the crab *Panopeus herbstii* feeding on the mussel *Brachidontes exustus* depends on predator and prey body size as well as the predator individual activity level. Photo credit: Kathryn Levasseur.


While the concept of consistent behavioural differences among individuals of the same population has gained a lot of scientific attention over the last decade, its implementation into a community context with a focus on species-level interactions is still in its infancy. In their study on the effects of animal personalities on predator–prey functional responses of mussel-eating crabs, Toscano & Griffen (2014) introduce a promising avenue for future research synthesizing concepts and ideas from animal behaviour and food web ecology. More precisely, by showing that the interplay of animal personalities and predator and prey body sizes significantly alters the outcome of predator–prey interactions, this study provides important evidence that the concept of animal personalities needs greater consideration if we want to refine and improve current models of predator–prey interactions and the impact of individual-level variation on quantitative food-web dynamics.

During recent years, it has been highlighted repeatedly that community-level studies focussing on species interactions (particularly food webs and other ecological networks) most often apply species or population averages for important traits (e.g. the trophic position of a consumer within a food web) and disregard intraspecific variation (Ings *et al.* 2009; Bolnick *et al.* 2011). The resulting knowledge gaps are critically affecting our understanding of predator–prey interactions that are vital for the structure and stability of communities as well as the mechanisms underlying important ecosystem services. For instance, due to the nonlinearity of predator–prey interaction strengths, the application of misleadingly derived average values might result in critical over- or underesti-
mation of feeding rates (‘Jensen’s inequality’: Okuyama 2008; Bolnick et al. 2011; Wolf & Weissing 2012). One might call intraspecific and ontogenetic variation in body size as the most evident example of such individual-level variation. Accordingly, body-size effects on trophic interactions and their dynamic consequences have been investigated intensively, improving our understanding of predator–prey population dynamics and community structure (e.g. Persson et al. 1998; Jansson et al. 2007; Hartvig, Andersen & Beyer 2011; Rudolf et al. 2014). On a mechanistic basis, insights into how body-size effects the predator–prey functional response (i.e. prey-density dependent per capita consumption rate) provides the link between individual behaviour and population dynamics (Wahlström et al. 2000; Kalinkat et al. 2013) when underpinned with biologically reasonable explanations (Brose 2010). Notably, Toscano and Griffen have previously investigated this relationship for their study system (Toscano & Griffen 2013) where body size and habitat structure interacted to determine the outcome and dynamics of predator–prey interactions, which is in line with another recent study for terrestrial invertebrates (Kalinkat et al. 2013).

However, body size does not explain everything (Rall et al. 2011; Boukal 2014; Rudolf et al. 2014). Therefore, the consideration and evaluation of other sources of intraspecific variation and their effects on species interactions is necessary. This is where consistent behavioural differences between individuals of a given population should also be acknowledged. The phenomenon of these so-called animal personalities (also termed behavioural types) was first described by Huntingford (1976) for aggression levels and boldness in three-spined sticklebacks without attracting much attention in the following two decades. From the late 1990s, however, research on animal personalities has skyrocketed (see Sih, Bell & Johnson 2004; Wolf & Weissing 2012 and references therein). The focus in most of these studies was set on documenting consistent individual variation in behavioural traits in a wide range of organisms and its proximate and ultimate causes (e.g. Biro & Stamps 2010) and how the puzzling evolutionary stability of this phenomenon might be explained (Wolf et al. 2007). Recently, however, there has been a rising interest in reinforcing the links between research on animal personalities and ecologically relevant research questions, including trophic interactions (Sih et al. 2012; Wolf & Weissing 2012; Boukal 2014).

The latest evidence available from laboratory (e.g. Sweeney et al. 2013) and field studies (e.g. Kobler et al. 2009) suggests that personalities significantly affect feeding rates and, hence, the interaction strengths in food webs. However, these tests remain rather phenomenological, and a better understanding of how the variation in behavioural traits affects the components of foraging and feeding behaviour mechanistically is still needed. This could in turn allow the implementation of a range of individual differences into advanced dynamic predator–prey population models. This approach seems particularly promising considering a recent study that applied the insights from empirical functional responses to parameterize such dynamic predator–prey models, which are then able to reproduce patterns at the community level with surprisingly high accuracy (Kalinkat et al. 2013).

In the endeavour of developing such advanced predator–prey population models that can incorporate individual differences in behaviour, the study of Toscano & Griffen (2014) provides a critical first step by showing that the relationship between individual variation in activity levels together with the body-size effects have a significant impact on the outcome of the crab–mussel interaction. To enhance the acknowledgement of individual variation in mechanistic models of predator–prey interactions, I propose future studies that combine functional responses with animal personalities incorporating a wider range of behavioural traits and their individual variation (e.g. activity levels, boldness and exploratory behaviour). Ideally, future approaches to determine the functional responses and its behavioural parameters (capture rate and handling time) should operate at the individual level as is the current standard for personality studies with their focus on among-individual variation. While Toscano & Griffen (2014) used the approach of traditional functional response studies, where focal mechanisms are usually investigated based on a priori defined subpopulations, individual measurements of capture rates and handling times in dependence of prey densities would then complement the high, individual-level resolution needed to resolve the relevant questions. This involves some technical and logistical difficulties that are not easily resolved, particularly for many short-lived taxa. Moreover, repeated measures of feeding rates with identical individuals would interact with a given habituation effect that should be considered in advanced statistical approaches.

In conclusion, I want to stress that these considerations might also have far-reaching practical and applied implications for management and conservation issues, further underlining the need to acknowledge and investigate them in the future. Beyond the basic question of what ultimately determines the outcome and dynamics of predator–prey interactions, the tremendous potential in behavioural type selective harvesting has already been documented theoretically (Alós, Palmer & Arlinghaus 2012), and it might impose drastic effects on exploited populations (Sutter et al. 2012). Hopefully, the incorporation of animal personalities into the food web context has just begun.

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