



Integrating trait multidimensionality, predation and autotomy to explain the maintenance of boldness



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There is an ongoing debate on how personality types are maintained within populations. We tested, for the first time, the potential of trait multidimensionality and trait compensation, where prey compensate for the costs of one trait by relying more on another one, in maintaining variation in boldness within a population. We studied how four boldness-related traits and swimming escape performance covary and shape the probability of survival and autotomy of *Ischnura pumilio* damselfly larvae in an experiment with predatory dragonfly larvae. Our results did not support the common belief that bold individuals are selected against in terms of survival selection by predation. Instead, we found survival selection favouring individuals combining being bold for two boldness-related traits. The four boldness-related traits did not covary frequently, supporting the multidimensionality of boldness. Moreover, animals bolder for one trait (activity in the presence of predator cues) were shyer for another trait (response to predator cues), which indicated trait compensation. However, the support for trait compensation was limited. The only other case of trait compensation was that bold larvae compensated for their increased risk-taking behaviour in the presence of a predator with a higher probability of autotomy. These patterns may contribute to maintaining variation in boldness in damselfly populations. Just as boldness-related traits are multidimensional, the mechanisms underlying their persistence in natural populations are also likely to be multifaceted.

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Individuals often differ consistently in behaviour (Réale, Reader, Sol, McDougall, & Dingemans, 2007). One striking widespread pattern is that some individuals within a population take more risks, hence are bold, than other, shy individuals (Dingemans & Wolf, 2010; Réale et al., 2007; Stamps & Groothuis, 2010). The mechanisms of persistence of such variation in personality traits within a population is highly debated (David & Dall, 2016; Réale, Dingemans, Kazem, & Wright, 2010). This is especially true for the persistence of boldness as bold individuals generally have a lower probability of survival in the presence of predators (Smith & Blumstein, 2008). Several mechanisms for the adaptive coexistence of personality traits have been suggested (Dingemans & Réale, 2005; Kight & Campus, 2013; Wolf & Weissing, 2010). One such mechanism is correlational selection on combinations of traits where different combinations can result in the same fitness (Dingemans & Réale, 2005). For example, predation favours both

the combination of bold and aggressive and that of shy and nonaggressive three-spined sticklebacks, *Gasterosteus aculeatus* (Bell & Sih, 2007).

An often overlooked factor when studying personality traits (Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013) is that these may be multidimensional. This has recently been explicitly shown for fear, as different fear-related variables did not covary in greenfinches, *Chloris chloris* (Sepp, Männiste, Kaasik, & Hórák, 2014). While we hypothesize that multidimensionality of boldness may contribute to its persistence in populations, this has not been tested. Because bolder prey rely less on antipredator behaviour, this is conceptually related to the well-known multidimensionality of antipredator behaviour where individuals can rely on different combinations of traits to reduce predation risk (DeWitt, Sih, & Hucko, 1999). Under such a scenario it may be misleading to study only one antipredator trait as individuals that rely less on this trait may compensate by relying more on other antipredator traits, resulting in the same level of defence against predators. This phenomenon has been called trait compensation of antipredator behaviours (DeWitt et al., 1999). We hypothesize that trait compensation may be at work not only within sets of boldness-

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related traits but also between boldness-related traits and other antipredator traits (e.g. antipredator morphology and escape performance). It could thereby generate correlational selection on combinations of personality traits, a selection mechanism suggested to maintain bold individuals in populations (Dingemanse & Réale, 2005). Two recent studies provided indirect support for trait compensation being at play in bold individuals. Bolder crucian carps, *Carassius carassius*, induced a stronger morphological defence against gape-limited predators (Hulthén, Chapman, Nilsson, Hollander, & Bronmark, 2013), and bolder brown anole lizards, *Anolis sagrei*, compensated for their risk taking by a higher propensity for autotomy (Kuo, Irschick, & Lailvaux, 2015). Neither study, however, evaluated the resulting survival value against predators which would further strengthen the case for trait compensation as a mechanism maintaining variation in boldness within populations.

To advance our knowledge of the still poorly understood persistence of bold individuals in populations (David & Dall, 2016; Réale et al., 2010; Smith & Blumstein, 2008), we here tested whether trait multidimensionality and trait compensation (DeWitt et al., 1999) play a role in mediating mortality by predation of bold larvae of the damselfly *Ischnura pumilio*. We did so by quantifying how a set of four boldness-related traits and escape performance covary, and individually and in combination shape the survival probability and the probability of autotomy in the presence of predators. The advantage of using damselfly larvae is that their antipredator defences are well known (e.g. Corbet, 1999; Stoks, McPeck, & Mitchell, 2003). Furthermore, personality traits have been identified in damselfly larvae (Brodin, 2008; Brown & Robinson, 2016), including *Ischnura* species (Debecker, Sanmartín-Villar, de Guinea-Luengo, Cordero-Rivera, & Stoks, 2016; Slos & Stoks, 2006). We quantified four boldness-related traits: swimming propensity when attacked (based on Strobbe, McPeck, De Block, & Stoks, 2009), activity in the presence of predator cues (Smith, Miner, Wiegmann, & Newman, 2009; Wilson & Godin, 2009), response to predator cues (Tüzün, Debecker, Op de Beeck, & Stoks, 2015), and latency time after escape swimming (Brodin, 2008; Debecker et al., 2016; Niemelä, DiRienzo, & Hedrick, 2012). These boldness-related traits were overall repeatable in a set of *Ischnura* species that included *I. pumilio* (Sanmartín-Villar, 2014). As an escape performance trait we quantified burst swimming speed which is important for damselfly larvae to escape predation by large invertebrate predators (Strobbe et al., 2009). Besides survival in the presence of predators we also looked at autotomy, which is an important antipredator mechanism in damselfly larvae. When damselfly larvae are too slow to swim away when attacked by a predator and are grasped, they can rely on the autotomy of their caudal lamellae as a last resort to avoid being killed (Stoks & De Block, 2000).

We tested two novel hypotheses that are directly relevant for the maintenance of bold individuals in populations. Our first hypothesis was that boldness is multidimensional; hence larvae are not consistently bolder for multiple boldness-related traits. Under the hypothesis of trait multidimensionality, we expect covariation between boldness-related traits such that individuals bolder for one trait are not bolder for another trait. Our second hypothesis was that trait compensation between boldness-related traits themselves and between boldness-related traits and performance (escape speed or autotomy) mitigates the mortality by predation of bold damselfly larvae. Under the hypothesis of trait compensation, we expect covariation between boldness-related traits and/or performance traits such that animals bolder for one trait are shyer for another boldness-related trait or have a higher performance.

METHODS

Ethical Note and Housing Conditions

For this experiment, no permits or animal care protocols were required by the Animal Ethics Committee of the University of Leuven because the study organisms were both invertebrates (the damselfly *I. pumilio* and the dragonfly *Anax imperator*). A permit to collect both species was obtained from the Flemish Agency for Nature and Forests (A.N.B.). Ten mated females of *I. pumilio* were collected with a butterfly net in August 2014 from each of three ponds in Belgium: Hove (51°9'28.48"N; 4°28'36.80"E), Montfort (51°7'50.38"N; 5°55'26.67"E) and Haasrode (50°50'17.36"N; 4°44'22.28"E). These are shallow and fishless ponds with larvae of the dragonfly *A. imperator* as top predator. The field-caught females were kept in the laboratory in plastic cups (200 ml) with wet filter paper as oviposition substrate. The filters with eggs were placed individually in 200 ml conditioned water (dechlorinated tap water conditioned with grass and straw for at least 6 days) in plastic containers (6.5 × 9 cm and 5 cm high) where the freshly hatched larvae were kept together to increase survival (De Block & Stoks, 2003). Ten days after hatching, larvae were allocated individually to plastic cups (200 ml) filled with 150 ml conditioned water. Throughout the experiment, the larvae were kept in cups with a water temperature of 19.20 °C ± 0.29 °C (mean ± SE; $N = 21$) and a 16:8 h light:dark regime. Damselfly larvae were fed *Artemia* nauplii ad libitum 6 days a week (mean ± SE: 205 ± 54 nauplii per portion, $N = 10$ portions counted). In total 10 *A. imperator* larvae were caught with a dip net in a shallow pond in Belgium, Huldenberg (50°49'9.66"N, 4°36'24.21"E). These were housed individually under the same laboratory conditions as the damselfly larvae. They were fed three times a week with five living *Chironomus riparius* midge larvae while not used in the predation experiment. To keep track of the identity, each larva was given a unique code by blackening two, four or six femurs or tibiae with a permanent marker (Staedtler Lumocolor 313 S). The coding did not affect the survival of the larvae during the exposure period (generalized linear model, effect of coding: $\chi^2_1 = 0.051$, $P = 0.82$). During the behaviour assays, the damselfly larvae were filmed to minimize disturbance by the observer. At the end of the experiment, the surviving damselfly larvae were euthanized by freezing after the predation experiment and the dragonfly larvae were released in their pond of origin.

Experimental Procedure

To test our predictions, we followed a two-step procedure. First, we scored escape swimming speed and the four boldness-related traits in all larvae in a series of behavioural assays. We started by quantifying escape swimming speed and swimming propensity. Thereafter, we performed the assays to score activity in the presence of predator cues, response to predator cues and latency time after escape swimming. An overview of the different boldness-related traits and their interpretation can be found in Table 1. Before the behavioural assays the larvae were weighed to the nearest 0.01 mg using an electronic balance (AB135-S, Mettler Toledo). Mean larval body mass was 20.39 mg (SE = 0.15 mg, $N = 240$ larvae). Second, we carried out a predation experiment with these larvae in which we tested for effects of escape swimming speed and the four boldness-related traits on the probability of survival and autotomy in the presence of a free-ranging predator.

Assay for Swimming Speed and Propensity

We measured escape swimming speed and swimming propensity following established protocols for damselfly larvae (speed:

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