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

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Highlights:

- Mechanisms maintaining bolder animals within populations are not fully understood
- We scored boldness traits and linked these to autotomy and mortality by predation
- Boldness-related traits did not frequently covary, indicating multidimensionality
- Bold individuals were not killed more by predators
- Bold larvae relied more on autotomy to compensate increased risk-taking behaviour

Abstract: There is an ongoing debate on how personality types are maintained within populations. We for the first time tested 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 data 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 frequently covary, 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 also the mechanisms underlying their persistence in natural populations likely are multifaceted.

Key words: antipredator behaviour, correlational selection, Odonata, animal personality, predation risk compensation.

Individuals often consistently differ in behaviour (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). One striking widespread pattern is that some individuals within a population take more risks, hence are bold, compared to other, shy individuals (Dingemanse & 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, Dingemanse, 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 (B. R. Smith & Blumstein, 2008). Several mechanisms for the adaptive coexistence of personality traits have been suggested (Dingemanse & 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 (Dingemanse & Réale, 2005). For example, predation favours both the combination of bold and aggressive, and of shy and non-aggressive threespined 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 (Sepp, Männiste, Kaasik, & Hõrak, 2014). While we hypothesize that multidimensionality of boldness may contribute to its persistence in populations, the multidimensionality of boldness 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 particular antipredator 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-related traits but also between boldness-related traits and other antipredator traits (e.g. antipredator morphology and escape performance). It thereby could generate correlational selection on combinations of personality traits, a selection mechanism suggested to maintain bold individuals in populations (Dingemanse and 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 (Hulthen, Chapman, Nilsson, Hollander, & Bronmark, 2013), and bolder brown anole lizards (*Anolis sagrei*) compensated their risk-taking by a higher propensity for autotomy (Kuo, Irschick, & Lailvaux, 2015). Both studies, however, did not evaluate 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 the still poorly understood persistence of bold individuals in populations (B. R. Smith & Blumstein, 2008; David & Dall, 2016; Réale, Dingemanse, Kazem, & Wright, 2010), 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; A. L. 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 (K. L. 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 are overall repeatable in a set of *Ischnura* species that included *I. pumilio* (I. Sanmartín-Villar, unpublished data). As 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 had following 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 covariations 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 covariations between boldness-related traits and/or performance traits such that animals bolder for one trait are shy for another boldness-related trait or have a higher performance.

METHODS

Ethical note

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 by the Flemish Agency for Nature and Forests (ANB). 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 six days) in plastic containers (6.5 x 9 x 5 cm³) where the freshly-hatched larvae were kept together to increase survival (De Block & Stoks, 2003). Ten days after egg hatching, larvae were allocated individually to plastic cups (200 mL) filled with 150 mL conditioned water. Throughout the entire experiment, the larvae were kept in cups with a water temperature of 19.20 °C ± 0.29 °C (mean ± SE; n = 21) and a photoperiod of L:D 16:8 h. Damselfly larvae were fed *Artemia* nauplii *ad libitum* six days a week (mean ± SE: 205 ± 54 nauplii per portion, n = 10 portions counted). In total ten *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). The *A. imperator* larvae 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 (generalised 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 of 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.

148 *Experimental procedure*

149 To test our predictions we followed a two-step procedure. In a first step, we scored escape
150 swimming speed and the four boldness-related traits in all larvae in a series of behavioural
151 assays. We started with quantifying escape swimming speed and swimming propensity.
152 Thereafter, we performed the assays to score activity in the presence of predator cues,
153 response to predator cues and latency time after escape swimming. An overview of the
154 different boldness-related traits and their interpretation can be found in Table 1. Before the
155 start of the behavioural assays the larvae were weighed to the nearest 0.01 mg using an
156 electronic balance (AB135-S, Mettler Toledo). Mean larval body mass was 20.39 mg
157 (SE = 0.15 mg, n = 240 larvae). In a second step, we carried out a predation experiment with
158 the phenotyped larvae of step 1 where we tested for effects of escape swimming speed and the
159 four boldness-related traits on the probability of survival and autotomy in the presence of a
160 free-ranging predator.

161 *Assay for swimming speed and swimming propensity*

162 We measured escape swimming speed and swimming propensity following established
163 protocols for damselfly larvae (speed: Stoks and McPeck 2006, propensity: Janssens and
164 Stoks 2012). The larvae were individually transferred to a plastic container (20 x 26 x 5 cm³)
165 filled with 600 mL conditioned water. Larvae were tapped five times on the abdomen with a
166 probe to simulate a predator attack, with each time 30 seconds of recovery time in between. If
167 the larvae did not swim during the first five taps, we continued the procedure until they swam
168 three times to record the swimming speed; these extra taps were not included in the
169 calculation of the swimming propensity. Trials were done in the absence of predator cues. A
170 previous study on *Ischnura* larvae showed that escape behaviour was not affected by the
171 presence of predator cues (Gyssels & Stoks, 2005). Moreover, using this procedure in the
172 absence of predator cues on larvae retrieved from field enclosures with predators (where cues

were present), survival selection by dragonfly predators on these traits was demonstrated (Strobbe et al., 2009; Swaegers, Strobbe, McPeck, & Stoks, 2017).

To estimate swimming propensity, the response to each of the first five simulated predator attacks was scored as 0 (did not swim away) or 1 (did swim away). The swimming propensity was calculated as the sum and thus varied between 0 (never swam away) and 5 (always swam away). Larvae that almost never swam away can be considered as bold, because swimming away in the presence of a dragonfly predator is an adaptive escape strategy (Strobbe et al., 2009).

To estimate escape swimming speed, the first three swimming bouts per larva were filmed at 33.5 frames per second with a digital camera (Basler Scout with a Rich FL-BC1214D-VG lens) connected to a computer using Streampix software v3.55.0 (NorPix Inc.). From these recordings the swimming speed (cm/s) was quantified by analysing the first 15 frames of each swimming bout using ImageJ v1.48 (Schneider, Rasband, & Eliceiri, 2012) with plugin MTrackJ v1.5.0 (Meijering, Dzyubachyk, & Smal, 2012). The average swimming speed of the three bouts per larva was used in the statistical analyses. Only larvae with three intact lamellae were used as damselfly larvae swim by moving their abdomen from side-to-side thereby using the three caudal lamellae at the end of the abdomen to generate thrust (McPeck, 2000).

Assay for activity in the presence of predator cues and the response to predator cues

The protocol to determine the activity in the presence of predator cues and the response to predator cues was based on Janssens and Stoks (2012). First, the activity was quantified in the absence of predator cues as the number of walks in a 7-minute observation period in a plastic container (6.5 x 9 x 3 cm³) filled with 75 mL conditioned water. Afterwards, the larva was transferred to a new plastic container and activity was quantified in the presence of 0.5 mL predator medium. We always applied this order to avoid carry-over effects of the predator medium.

The preparation of predator medium was based on Mortensen and Richardson (2008) and Janssens, Dinh Van, Debecker, Bervoets, & Stoks (2014). It consisted of 0.5 mg of *Ischnura* wet mass per mL water and was prepared by homogenizing larvae and diluting the homogenate in dechlorinated tap water from an aquarium where an *Anax* larva had eaten two *Ischnura* larvae. The predator medium was frozen in small aliquots until use. Before each trial, the larvae could acclimatise for seven minutes in the container before the observation started. At the start of each 7-min observation trial (both in the absence and in the presence of predator cues) a portion of *Artemia* nauplii (mean $\pm$ SE: 244 ± 13 nauplii per portion, $n = 10$ portions counted) was added to stimulate activity of the *Ischnura* larvae. The hunger level of the *Ischnura* larvae was standardised by starving them for 24 hours before the behavioural assays. Four larvae were recorded simultaneously from above with a full-HD camera (Sony HDR-CX240). Afterwards, these recordings were observed with VLC Media Player v2.1.5 (Free Software Foundation, Inc.). Given the relatively short observation times, no satiation occurs during the second observation period in coenagrionid damselfly larvae, so any reductions in activity during the second observation period can be directly interpreted as antipredator behaviour (Janssens & Stoks, 2012).

Larvae with a high activity in the presence of predator cues can be considered as bold (K. L. Smith et al., 2009; Wilson & Godin, 2009). Based on the activity measures of both successive observations of the same larvae we calculated the response to predator cues as $[(\text{activity in presence of the predator medium}) - (\text{activity in absence of the predator medium})] / (\text{activity in absence of the predator medium})$ (Hulthén et al., 2013). Larvae with a weak response to predator cues can be considered as bold (Tüzün et al., 2015). While activity in the presence of predator cues is an absolute measure of activity, the response to predator cues represents the relative change in activity in response to the predator cues. Both have been used before as measures of boldness (K. L. Smith et al., 2009; Tüzün et al., 2015; Wilson & Godin, 2009) and contain different information. The absolute activity in the presence of

predator cues directly determines the chance of being detected by the sit-and-wait predator and has been shown to be a predictor of survival times in the presence of dragonfly predators (Janssens et al., 2014; Janssens & Stoks, 2012). The response to predator cues instead reflects how much an individual is responding to the predator compared to its baseline activity. Depending on the baseline activity in the absence of predator cues, weak or strong responses to predator cues may result in the same activity level in the presence of predator cues.

Assay for latency time after escape swimming

To quantify latency time after escape swimming, the larvae were transferred to an opaque aquarium (11 x 7 x 11.5 cm³) filled with 250 mL conditioned water and 1.3 mL predator medium. The larvae could acclimatise for seven minutes and were then tapped on the abdomen with a probe to simulate a predator attack. Sessions were videotaped and analysed afterwards. The time that the larva remained motionless after swimming in response to the simulated predator attack was defined as the latency time (based on Brodin 2008). Larvae with a short latency time after escape swimming can be considered bold (Brodin, 2008; Debecker et al., 2016).

Predation experiment

To test for effects of antipredator traits (boldness-related traits and escape swimming speed) on the probability of survival and autotomy we ran a predation experiment in which sets of 20 *I. pumilio* larvae were exposed to a predatory dragonfly larva in aquaria. The predation experiment was executed using final instar larvae with three intact lamellae. As predators, we chose larvae of the dragonfly *Anax imperator* (body size: mean $\pm$ SE: 42.69 $\pm$ 2.19 mm, n = 18), which are important predators of *Ischnura* larvae (Stoks et al., 2005).

Predation trials took place in opaque aquaria (22 x 47 x 26 cm³) filled with 20 L of conditioned water. To each aquarium 30 artificial plants, consisting of two ribbons of green plastic net (2 x 20 cm, mesh size 2 mm) tied together around a stainless-steel screw with a tie-

wrap, were provided as structure. Three days before the trials started, *Ischnura* larvae were placed in the aquaria with the caged *Anax* predator. The cage was a transparent Plexiglass cylinder (7.4 cm diameter, 20 cm height) with three openings covered with a filter (mesh size 500 μ m), that was placed in the centre of each aquarium. The openings in the cylinder allowed flow-through of water and dissolved substances. During the period that the *Anax* predator stayed in the cage, it was fed a final instar *Ischnura* larva twice a day to release conspecific cues and five *Chironomus riparius* midge larvae. This way, the *Ischnura* larvae received both visual and chemical stimuli of both the predator and conspecifics. After three days, the *Anax* predator was released from the cage and could start hunting damselfly larvae. We ran 12 predation trials (total of 240 larvae). Each trial contained larvae from the three populations. A predation trial was ended when ca. 10 (mean $\pm$ SE: 9.08 ± 0.38 , $n = 12$ aquaria) out of the 20 larvae (ca. 50%, cfr. Bell & Sih 2007) were consumed; this took ca. 1.5 days (1.58 ± 0.26 days, $n = 12$ trials).

The damselfly larvae were fed twice a day *ad libitum* *Artemia* nauplii in the aquaria (4097 ± 1071 nauplii per portion; $n = 10$ portions counted). For each of the surviving larvae we quantified the number of lamellae.

Statistical analyses

All statistical analyses were performed in R v3.1.1. (R Core Team, 2015) with the packages lme4 v1.1-7 (Bates, Maechler, Bolker, & Walker, 2015) and car v2.0.25 (Fox & Weisberg, 2011). To meet model assumptions, activity and the response to predator cues were $\text{Log}_{10}(x+1)$ -transformed and latency time after escape swimming was $\text{Log}_{10}(x)$ -transformed. Because in the predation trials we used sets of 20 larvae per aquarium, aquarium was added as a random factor in all the statistical models. Larvae from the three populations and from different families were used per trial. Population and family nested in population were therefore also added as a random factor in all models. The models testing for effects of

antipredator traits on the probability of autotomy only included the damselfly larvae that survived the predation trials.

To test whether the five antipredator traits (four boldness-related traits and escape performance) covaried and whether these patterns differed between groups (based on survival status or autotomy status), we used linear mixed models (LMMs) each time including one antipredator trait pair. Thus, they included each time one antipredator trait as dependent variable and another antipredator trait as covariate. These models included survival or autotomy status as the fixed group factor. Finally, the interaction between this covariate and the fixed factor was included to test whether the covariation patterns differed between groups. The specific choice of which antipredator traits were considered the dependent or the independent variable in these analyses did not affect the conclusions. Therefore, results of only one of the two analyses is presented. P-values were corrected for the false discovery rate. A matrix with all pairwise correlations between the five traits is presented for all larvae in the supplementary Table S1. Both the uncorrected as the false discovery rate corrected p-values are shown in the matrix. The means and standard errors for all behaviours are shown in the supplementary Table S2.

To test whether the antipredator traits and their pairwise combinations determined the probability of survival in the predation trials, we used generalised linear mixed models (GLMMs) with a binomial error structure and the logit link (based on Bell & Sih 2007). Survival was coded binary with 1 for larvae that survived and 0 for larvae that did not survive. To measure the strength of the selection coefficients, linear mixed models were used with a normal error structure, the identity link and standardised independent variables (Lande & Arnold, 1983). The relative fitness was used as dependent variable and was calculated as the absolute binary fitness divided by the average fitness of the larvae in a given aquarium (cfr. Mikolajewski et al., 2006). In a first step, we tested for univariate directional selection by including all five antipredator traits as predictors in a single model. Next, non-linear selection

was tested by including all five traits and their squared terms as predictors in a single model. Finally, correlational selection on trait combinations was tested in a two-step approach to ensure interpretability. Initially, we included each time two of the five antipredator traits and their interaction as predictors in a single model. Thereafter, we combined the significant pairwise interactions and the associated single traits in a joint analysis to see if the significance of the identified effects was robust. Significant cases of correlational selection were visualised by surface plots using the distance weighted least squares. A similar approach was used to test whether antipredator traits and their pairwise combinations predicted the probability of autotomy. Autotomy was also coded binary with 1 for larvae that lost at least one lamella and 0 for larvae that kept all lamellae. These models were run with body mass as covariate to correct for mass differences between the larvae.

RESULTS

In total 109 of the 240 larvae survived the predation trials. Of these survivors 40 larvae still had all three lamellae, hence did not rely on autotomy.

Covariation patterns between antipredator traits

Between the five antipredator traits studied, there were only two (out of ten possible) significant covariation patterns that were consistent between survivors and non-survivors: a negative association between latency time after escape swimming and activity in the presence of predator cues (LMM: $\chi^2_1 = 14.47$, $P < 0.001$, slope $\pm$ SE = -0.36 ± 0.16) and a positive association between activity and response to predator cues (LMM: $\chi^2_1 = 92.90$, $P < 0.001$, 0.57 ± 0.07) (for all other combination: $P \geq 0.17$). For two other trait combinations, there was a covariation pattern that differed between survivors and non-survivors. While there was a trend that non-survivors showed a negative covariation between escape swimming speed and response to predator cues (slope $\pm$ SE = -0.59 ± 0.32 , $P = 0.067$), there was no pattern for

survivors (0.50 ± 0.36 , $P = 0.16$) (LMM: response $\times$ survival: $\chi^2_1 = 5.79$, $P = 0.081$, regression lines in Figure 1a). While survivors showed a negative covariation between swimming propensity and activity (-0.79 ± 0.37 , $P = 0.032$), non-survivors showed the opposite pattern (0.68 ± 0.33 , $P = 0.042$) (LMM: activity $\times$ survival: $\chi^2_1 = 8.38$, $P = 0.038$, regression lines in Figure 1b). Within the group of survivors, there was no trait combination that showed a significant covariation pattern between both autotomy groups (all $P \geq 0.32$).

Determinants of survival

The GLMMs showed that predation by the dragonfly larvae did not impose directional selection on any of the antipredator traits of *I. pumilio* larvae, except for a trend for positive directional selection on the response to predator cues ($P = 0.083$) and on escape swimming speed ($P = 0.053$, Table 2a). However, both traits were also under correlational selection (swimming speed $\times$ response, Table 3a). Survival was higher when larvae swam fast and had a strong response to predator cues (shy) (Figure 1a). There were no larvae that combined extreme values for both swimming speed and the response to predator cues (Figure 1a). We also detected correlational selection on the combination of swimming propensity and activity in the presence of predator cues (swimming propensity $\times$ activity, Table 3a). The survival probability was highest when the larvae (almost) never swam away and simultaneously had a high activity, and lowest when the larvae (almost) never swam away and simultaneously had a low activity (Figure 1b). Furthermore, larvae that (almost) always swam away had an average probability of survival independent of their activity. We never detected quadratic selection on the antipredator traits (Table 2b, all $P \geq 0.21$).

Determinants of lamellae autotomy

The GLMMs showed that within the subset of survivors the probability of autotomy was not determined by individual antipredator traits, except for a positive trend of swimming propensity ($P = 0.060$, all other $P \geq 0.11$, Table 2a). However, the probability of autotomy

was jointly shaped by swimming propensity and the response to predator cues (swimming propensity $\times$ response, Table 3b). The probability of autotomy was highest when larvae frequently swam away (never swam away) and simultaneously had a strong (weak) response to predator cues (Figure 2a). Furthermore, the probability of autotomy was highest when larvae had a short latency time after escape swimming and simultaneously had a strong response to predator cues (latency time $\times$ response, Table 3b, Figure 2b). There were no larvae that combined extreme values for both latency time and the response to predator cues (Figure 2b). No quadratic trait effects on autotomy were observed, except a trend for latency time ($P = 0.070$, Table 2b, all other $P \geq 0.18$).

DISCUSSION

It was apparent that although we studied four traits that are considered measures of boldness (e.g. Brodin 2008; K. L. Smith et al., 2009; Strobbe et al., 2009; Tüzün et al., 2015), these traits did not frequently covary so that animals bolder for one trait were typically not bolder for another trait, thereby supporting our first hypothesis of the multidimensional nature of boldness (cfr. Sepp et al., 2014 for fear). Thus, if only one boldness-related trait would have been studied, the conclusion would differ according to which of the boldness-related traits would have been chosen.

We found little further support for our second hypothesis of trait compensation, where prey compensate the costs of one trait by relying more on another one (DeWitt et al., 1999), with regard to boldness. One covariation pattern that was significant across all larvae showed a coupling where animals bolder for one trait (a higher activity with predator cues) were shyer for the other trait (a stronger response to predator cues), which indicated trait compensation. The only other case of trait compensation was that bold larvae did compensate for their increased activity in the presence of a predator with a higher probability of autotomy. We also found an indication for trait cospecialization, where prey consistently rely on two independent

antipredator traits to defend themselves (DeWitt et al., 1999): larvae with a strong response to predator cues (shy) tended to have a higher escape speed. Another striking finding was that trait combinations rather than single traits contributed to survival or autotomy, indicating correlational selection to be more important than directional selection.

Determinants of survival

As shown before in another damselfly species (Strobbe, McPeck, De Block, & Stoks, 2010) larvae with a higher escape swimming speed tended to have a higher chance of survival. This is expected as damselfly larvae can reduce the chance of being captured by dragonfly larvae by swimming away (McPeck, 1990; Stoks & De Block, 2000). However, correlational analyses indicated this was only the case when larvae with a high escape swimming speed had a strong response to predator cues (hence were shyer). This does not match a pattern of trait compensation but rather a pattern of trait cospecialization (DeWitt et al., 1999) where prey organisms that combine both antipredator traits are better in dealing with predation. A possible explanation that a high escape swimming speed alone is not enough to have the highest probability of survival, is that *I. pumilio* is a species with a relative low escape swimming speed (mean $\pm$ SE: 9.80 ± 0.08 cm/s, $n = 240$ larvae) compared to other damselfly larvae (Stoks & McPeck, 2006). We hypothesise that the correlational selection arises because shy larvae (here: those showing a strong response to predator cues) might have been more vigilant and started their escape swim earlier.

Surprisingly, when *I. pumilio* larvae combined being bold for two boldness-related traits, i.e. when they (almost) never swam away and had a high activity in the presence of predator cues, they had the highest survival probability. This pattern does not match trait compensation. A possible explanation for this counterintuitive result is that larvae with a high activity that did not swim away, were bold enough to slowly retreat when they detected the predator (yielding higher activity scores, V. Delnat, personal observation) instead of remaining immobile because of fear. Vice versa, larvae that had a low activity and did

(almost) not swim away, stayed in a close range of the nearby predator which may have decreased their probability of survival. This might also explain why the probability of survival is independent of activity when larvae had a high swimming propensity. Here, the larvae always swam away and escaped or got killed by the predator, making the level of activity (presumably retreating or not) less relevant at that crucial moment. A possible reason for the absence of the expected pattern that a high swimming propensity results in a higher probability of survival (Strobbe et al., 2009), is that *I. pumilio* is a species with a relative low escape swimming speed, as discussed above.

Determinants of lamellae autotomy

Autotomy, the release of a body part, is a widespread escape mechanism when grabbed by a predator (Fleming, Muller, & Bateman, 2007). While autotomy involves a reflex process, the propensity for autotomy is also believed to be under conscious control in several taxa (e.g. Kuo et al., 2015), including damselfly larvae (Gleason, Fudge, & Robinson, 2014). The combination of swimming propensity and response to predator cues determined the probability of autotomy (similar to correlational selection). Damselfly larvae with a strong response to predator cues (i.e. shy larvae) still had an increased probability of autotomy when they (almost) always swam away. However, when the response was weak, larvae that (almost) never swam away had a higher probability of autotomy. Assuming a conscious component in lamellae autotomy in damselfly larvae (Gleason et al., 2014), this indicates that bold larvae compensated for their increased risk-taking behaviour in the presence of a predator with a higher probability of autotomy, consistent with a scenario of trait compensation (DeWitt et al., 1999). This is partly in accordance with the study of Kuo et al. (2015) where bold lizards autotomised their tail more readily.

The other antipredator trait combination that tended to determine the probability of autotomy, was the combination of latency time after escape swimming and response to predator cues. In general, larvae with a short latency time are expected to rely more on

autotomy, because there is a realistic chance that the predator that elicited the previous escape response is still nearby and alert, whereas after a long latency time after escape swimming the predator might have lost interest and/or moved away. We found a signal of this expected effect of latency time on autotomy, yet apparently only for shy damselfly larvae (here: larvae with a strong response to predator cues).

Conclusions

There is an ongoing debate on how personality types are maintained within populations (Dingemanse & Réale, 2005; Kight & Campus, 2013; Wolf & Weissing, 2010). Especially, the persistence of bold and shy individuals in a population has been intensively studied (e.g., C. Brown, Jones, & Braithwaite, 2005; Hulthen et al., 2013; Magnhagen et al., 2014; Niemelä, DiRienzo, et al., 2012; Ward, Thomas, Hart, & Krause, 2004; Wilson & Godin, 2009). Our results add three important novel insights to this debate. First, we are the first to explicitly document that boldness is multidimensional, and we even documented a pattern where animals bolder for one trait were shyer for another one (hypothesis 1). Second, we found little support for our novel second hypothesis that trait compensation (DeWitt et al., 1999) may play a role in maintaining bold individuals in populations. Moreover, we also found support for trait cospecialization (DeWitt et al., 1999) between one boldness-related trait and escape speed. Third, a last important insight was that our data did not support the common belief that bold individuals are selected against in terms of survival selection by predation. Instead, we found correlational survival selection favouring individuals combining two boldness-related traits. While some of the here reported patterns may contribute to maintaining variation in boldness in damselfly populations, likely also other mechanisms are contributing (Dingemanse & Réale, 2005; Kight & Campus, 2013; Wolf & Weissing, 2010). Just as boldness-related traits are multidimensional also the mechanisms underlying their persistence in natural populations likely are multifaceted.

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602 **TABLES**

603

604 Table 1. Overview of the four boldness-related traits.

Boldness-related trait	Description	Trait value indicating bolder individuals	Reference
Swimming propensity	Number of times (out of 5) the larvae swims away in response to a simulated predator attack	Low	Strobbe et al. (2009)
Activity in the presence of predator cues	Number of walks in a 7-minute observation period	High	K. L. Smith et al. (2009) Wilson & Godin (2009)
Response to predator cues	Relative change in the number of walks between 7-min observation periods in the absence and in the presence of predator cues	Weak	Tüzün et al. (2015)
Latency time after escape swimming	Time a larva remains motionless after swimming in response to a simulated predator attack	Short	Brodin (2008) Debecker et al. (2016) Niemelä et al. (2012)

605

Table 2. The results of the univariate generalised linear mixed models (χ^2_1 and P-values) testing for the effects of the five antipredator traits on the probability of survival and the probability of autotomy. Shown are the results for the linear terms (a) and for the quadratic terms (b). In the models to test for the quadratic terms also the linear terms were included, yet to increase readability these are not reported. Note that the estimates of the relationships (β , $\gamma/2$ and SE) are derived from related univariate linear mixed models with the relative fitness (as recommended by Lande and Arnold, 1983). Survival and autotomy were coded as binomial response variables.

	Survival				Autotomy			
(a) Linear terms	χ^2_1	P	β	SE	χ^2_1	P	β	SE
Swimming propensity	0.94	0.33	-0.06	0.07	3.55	0.060	0.11	0.09
Swimming speed	3.75	0.053	0.16	0.07	0.02	0.90	-0.03	0.09
Latency time	1.53	0.22	-0.05	0.07	0.01	0.94	0.01	0.09
Activity with predator cues	0.79	0.37	0.05	0.07	0.56	0.46	0.03	0.09
Activity response	3.00	0.083	0.11	0.07	0.07	0.79	-0.03	0.09
	Survival				Autotomy			
(b) Quadratic terms	χ^2_1	P	$\gamma/2$	SE	χ^2_1	P	$\gamma/2$	SE
Swimming propensity ²	1.51	0.22	-0.07	0.06	0.44	0.51	0.01	0.08
Swimming speed ²	0.14	0.71	0.01	0.05	0.18	0.67	-0.07	0.07
Latency time ²	1.60	0.21	0.09	0.06	3.29	0.070	-0.17	0.09
Activity with predator cues ²	0.03	0.87	-0.01	0.06	0.67	0.41	-0.09	0.07
Activity response ²	0.37	0.54	-0.02	0.04	1.82	0.18	-0.05	0.05

Table 3. The results of the generalised linear mixed models testing for the effects of the five antipredator traits and their pairwise combinations on (a) the probability of survival and (b) the probability of autotomy. In all models also the linear terms were included, yet to increase readability these are not reported. Besides separate models per pairwise combination, also the results of the joint model with all pairwise combinations identified to be significant in the separate models are given. Note that the estimates of the relationships (γ and SE) are derived from related univariate linear mixed models (as recommended by Lande and Arnold, 1983). Significant P-values ($P < 0.05$) are indicated in bold.

(a) Survival	Separate models				Joint model			
	χ^2_1	P	γ	SE	χ^2_1	P	γ	SE
Swimming propensity $\times$ Swimming speed	0.59	0.44	-0.04	0.05				
Swimming propensity $\times$ Latency time	2.20	0.14	0.10	0.07				
Swimming propensity $\times$ Activity	5.82	0.016	-0.17	0.07	5.78	0.016	-0.20	0.08
Swimming propensity $\times$ Activity response	1.24	0.26	-0.08	0.07				
Swimming speed $\times$ Latency time	0.29	0.59	-0.04	0.07				
Swimming speed $\times$ Activity	0.41	0.52	0.04	0.06				
Swimming speed $\times$ Activity response	5.67	0.017	0.17	0.08	5.80	0.016	0.18	0.09
Latency time $\times$ Activity	1.24	0.27	-0.06	0.07				
Latency time $\times$ Activity response	0.07	0.80	-0.01	0.08				
Activity $\times$ Activity response	0.24	0.62	-0.02	0.06				
(b) Autotomy	Separate models				Joint model			
	χ^2_1	P	γ	SE	χ^2_1	P	γ	SE
Swimming propensity $\times$ Swimming speed	0.01	0.91	-0.02	0.08				
Swimming propensity $\times$ Latency time	0.03	0.85	0.01	0.09				
Swimming propensity $\times$ Activity	2.02	0.15	0.11	0.10				
Swimming propensity $\times$ Activity response	4.68	0.030	0.14	0.09	4.29	0.038	0.13	0.09
Swimming speed $\times$ Latency time	0.49	0.48	-0.01	0.09				
Swimming speed $\times$ Activity	2.52	0.11	0.12	0.10				
Swimming speed $\times$ Activity response	0.11	0.74	-0.03	0.11				
Latency time $\times$ Activity	1.46	0.23	0.10	0.09				
Latency time $\times$ Activity response	4.29	0.038	-0.13	0.11	3.10	0.078	-0.10	0.11
Activity $\times$ Activity response	1.12	0.29	-0.09	0.08				

FIGURE LEGENDS

Figure 1. Surface plots showing how pairwise combinations of antipredator traits determine the probability of survival in the presence of dragonfly predators: (a) escape swimming speed $\times$ response to predator cues and (b) swimming propensity $\times$ activity in the presence of predator cues. Activity and response were $\text{Log}_{10}(x+1)$ transformed. Survival was coded as a binomial response variable. Darker colours represent regions with a higher probability of survival. White (black) dots represent the observed values of the survivors (non-survivors). Single dots may represent multiple observations. Percentages of larvae in each quartile are shown. The white (black) dotted lines are the fitted regression lines of the survivors (non-survivors), lines in bold are significant.

Figure 2. Surface plots showing how pairwise combinations of antipredator traits determine the probability of autotomy: (a) swimming propensity $\times$ response to predator cues and (b) latency time after escape swimming $\times$ response to predator cues. Activity and response were $\text{Log}_{10}(x+1)$ transformed, while latency time was $\text{Log}_{10}(x)$ transformed. Autotomy was coded as a binomial response variable. Darker colours represent regions with a higher probability of autotomy. White (black) dots represent the observed values of the larvae with less than three lamellae (larvae with three lamellae). Single dots may represent multiple observations. Percentages of larvae in each quartile are shown. The white (black) dotted lines are the fitted regression lines of the larvae with less than three lamellae (larvae with three lamellae), lines in bold are significant.

FIGURES

Figure 1.

652 Figure 2.

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