

Sex and size matters: Selection on personality in natural prey-predator interactions



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ABSTRACT

Optimal life-history strategies are currently considered to be a major driving force for the maintenance of animal personalities. In this experimental study we tested whether naturally occurring predation causes personality-dependent mortality of a marine isopod (*Idotea balthica*), which could maintain personality variation in nature. Moreover, as isopods are known to have sex-differences in behaviour, we were interested in whether personality-dependent predation was sex-specific. We also hypothesised that predation pressure among personality types could vary according to habitat type, as it has been shown in correlative studies that habitat may influence personality variation. We used natural predator (European perch *Perca fluviatilis*) of *I. balthica* and studied relative mortality of males and females with a different personality types in laboratory settings with two different habitats. We found that survival in males was lower than in females for high active individuals. Moreover, survival under predation was linked to body size differently in females and males. This, however, depended on personality class as larger size was advantageous for low-active males and middle- and high-active females. Conversely, smaller size was advantageous for low-active females and middle-active males. Size did not affect survival in high-active males. Our results suggest that predation can encourage life-history differences between sexes leading to different optimal life-history strategies and also maintains consistent activity for both sexes.

1. Introduction

Consistent individual differences i.e. animal personalities have been reported for a wide range of species across the animal kingdom, including mammals, fishes, birds, reptiles, amphibians, arthropods and molluscs (reviewed by Bell et al., 2009; Dall and Griffith, 2014). There is accumulating evidence that variation in personality traits is ecologically and evolutionary meaningful (Sih et al., 2004a; Sih et al., 2004b; Réale et al., 2007; Wolf and Weissing, 2012), as for instance, individual personality variation is coupled with fitness (meta-analysis by Smith and Blumstein, 2008) and it has an important role in mediating intra- and interspecific competition and dynamics of ecological networks (reviewed in Wolf and Weissing, 2012). As any trait related to fitness, selection on personality is assumed to be stabilising but with an optimum that varies periodically and stochastically (Burger and Gimelfarb, 2002). However, personality variation has often remained in populations. On account of this, to explain personality variation found in nature, we need to understand the mechanism associated with evolution of personality traits.

Personality variation is associated with life-history traits such as

reproductive success and survival (reviewed in Wolf and Weissing, 2012). The between-individual variation in optimal life-history strategies (Biro and Stamps, 2008; Réale et al., 2010) and in life-history trade-offs (Stamps, 2007; Wolf et al., 2007) is currently considered to be a major driving force for the maintenance of animal personalities. Selection pressures drive differences in life-histories and can vary between the sexes (sexual antagonistic selection), which can maintain personality variation (Dingemanse et al., 2004; Dingemanse and Réale, 2013; Pruitt et al., 2008; Pruitt and Riechert, 2009; Patrick and Weimerskirch, 2014) or lead to sexual dimorphism in personality (Schurch and Heg, 2010). Sexual antagonistic selection occurs when phenotype and fitness are negatively correlated across the sexes, such that values of the trait that are related to low fitness of males are also associated with high fitness of females and *vice versa* (Chippindale et al., 2001). For example, in great tits (*Parus major*) adult annual survival was dependent on personality and sex. Fast-exploring females had higher survival than slow-exploring females in years with low food availability, whereas fast-exploring males had higher survival than slow-exploring males when the food supply was high (Dingemanse et al., 2004). Further, Patrick and Weimerskirch (2014) found that shy

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black browed albatross (*Thalassarche melanophrys*) females who forage further from the colony, in deeper oceanic waters, have higher breeding success in poor quality years, whereas bold males foraging close to the colony in shallower regions always have higher breeding success. Sexual antagonistic selection has been also shown in a study with comb-footed spiders (*Anelosimus studiosus*) as asocial males had better mating success compared to social males, and this trend was opposite in females (Pruitt et al., 2008; Pruitt and Riechert, 2009). These studies show that sex-specific selection is associated with personality variation in animals.

Predation is a well-documented force behind differential selection patterns between personality types (Réale and Festa-Bianchet, 2003; Dingemans and Réale, 2005; Kortet et al., 2010). In general, however, most studies on personality-dependent predation have focussed on pooled data from both sexes. Furthermore, previous work has concentrated on relations between predation and personality by studying survival of personality types with correlative data using the “capture-release-recapture” method in nature (e.g. Réale and Festa-Bianchet, 2003). Moreover, previous studies have mainly concentrated on measuring individual personality differences collected from environments with known variation in predation pressures (e.g. Brown et al., 2005; Brown et al., 2007), and knowledge from experimental studies is lacking (but see Smith and Blumstein, 2010; Krams et al., 2013a,b).

It has been hypothesised that spatially varying predation pressures can induce population divergence in personality. For example, Brown et al. (2005, 2007) found that fish from populations with high and low levels of predation risk differed in their boldness. These results suggest that spatial variation in predation could play a significant role in shaping personality variation. On account of this, personality variation within a species could be maintained by varying selection pressures among environments. Environmental conditions can also offer different cognitive stimuli for predators if the physical characteristics of habitats vary. This can lead to fluctuating personality-dependent predation if selection favours different personality types in different environments, which can lead to population divergence in personality. This theory has not been studied coupled with sex-differences before.

In this study, we examined experimentally the importance of predation by the perch (*Perca fluviatilis*), a common predatory fish, on inducing selective force on the personality of the marine isopod *Idotea balthica*. An earlier study on *I. balthica* has shown that activity is a personality trait, with evidence of consistent behaviour over time measured as repeatability (Yli-Renko et al., 2015). Moreover, personality is related to overwintering survival in laboratory settings (without predators present), suggesting individual differences e.g. in energy metabolism, may promote individual differences in behaviour (Yli-Renko et al., 2015). In this study, we specifically investigated whether (a) predation is personality dependent; (b) the sexes have different personality optima under predation; and (c) personality-dependent predation varies in different physical environments

2. Materials and methods

2.1. Study species

The isopod *I. balthica* is a colour polymorphic, generalist herbivore of macrophytes (Salemaa, 1978; Salemaa, 1979). In our study area in the Northern Baltic Sea (locational details below), it occurs frequently in stands of rockweed (*Fucus vesiculosus*) but it is also found in meadows of *Zostera marina* (Bostrom et al., 2006). In the Northern Baltic Sea, *I. balthica* has a lifespan of 13–15 months (Salemaa, 1979) and it has only one breeding season, without overlapping generations. In the Northern Baltic the population consists of four main phenotypes: uniformly coloured uniformis, white-spotted albafulca, fine-mottled maculata and two- or three-striped lineata (Salemaa 1978; Vesakoski 2009b)

Idotea balthica is sexually dimorphic in morphology, physiology and behaviour. For example, it has strong sexual variation in activity during

reproductive periods when males are the more active sex (Jormalainen and Tuomi, 1989; Vesakoski et al., 2008). Males are larger than females (Salemaa, 1979) and during the day males are bolder compared to females (Yli-Renko et al., 2015). In adult *I. balthica*, sexes prefer different microhabitats so that females are found at the lower parts of *F. vesiculosus* thalli more often than males partly because the lower parts likely provide better shelter (Merilaita and Jormalainen, 2000) and partly because female growth is not as sensitive to phlorotannin compounds of the lower parts as male growth is (Jormalainen et al., 2001). Due to differences in trade-offs between shelter and food, it is inferred that males are more risk-prone in their behaviour whereas females are more risk-averse (Vesakoski et al., 2008).

Besides sexual variation within the species, behaviour of the isopods also depend on the living environment of the local population. This has been studied with populations associated with *F. vesiculosus* dominated algal assemblages and *Z. marina* dominated meadows of vascular plants. Isopods associated to these two environments differ in host use abilities (Vesakoski et al., 2009a; Mattila et al., 2014), host preferences (Vesakoski et al., 2009a) and even differing colouration (Vesakoski, 2009b). In this study, we used this prior knowledge of the two habitats performing differing selection environments by building the aquaria to mimic the two visually different predatory regimes.

2.2. Field collections

In November 2009, we sampled 283 isopods (140 females; mean size: 34 mg ± 16 mg and 143 males; mean size 55 mg ± 32 mg) from two locations (*F. vesiculosus* and *Z. marina* habitats) in the vicinity of the Archipelago Research Institute (60°14'N, 21°57'E, University of Turku) and Tvärminne Zoological station (59°50'N, 23°14'E, University of Helsinki). We chose these populations as we knew they would harbour isopods with large variation of different colour morphs (Vesakoski, 2009b). The earlier site is *F. vesiculosus* habitats with lots of spotted individuals (*albafusca*, see below) and the latter one is *Z. marina* habitat with both *albafusca*-individuals and striped *lineata*-individuals. The animals were transported immediately to the laboratory. Isopods were juveniles aged 3–5 months, having reached almost adult size, but not sexual maturity.

Prior to the experiments, we maintained the isopods for two weeks in groups of 30–40 in 20 l aerated aquaria with standing brackish water (salinity 5–6 ppt) and *F. vesiculosus* as food and habitat. We maintained them in a temperature-controlled laboratory (7–8 °C) and the light regime was 10Light:14Dark, similar to natural conditions in the current season. Before the experiment, we weighed the isopods and determined their sex and colour morph following Jormalainen and Tuomi (1989). Finally, we photographed the isopods to be able to identify them individually at the end of the experiment. After taking the measurements, we placed the isopods individually in 200 ml glass jars with standing brackish water in the same temperature and light regime as before, and with a segment of *F. vesiculosus* as food and shelter.

2.3. Measuring activity

We conducted activity measurements in aquaria with 2.7 l standing brackish water at 7–8 °C (salinity 5–6 ppt). Aquaria (w: 23 cm, d: 13 cm, h: 14 cm) had sand and a small stone on the bottom to provide a habitat. An ‘apical’ (growing tip) and a ‘basal’ (old thallus part) piece of the brown alga *F. vesiculosus* were placed at opposite ends of the aquaria to provide shelter and food. Each individual remained in their own aquaria throughout the activity measurements. We first left the isopods to acclimate in the aquaria for 12 h to make sure we were measuring activity instead of exploration behaviour in a novel environment. We measured activity for all 283 individuals by monitoring the location of each individual once every 50 min and calculating how many times the isopod had changed its position during the experiment. An isopod could be in one of the following positions: interacting with the ‘apical’ or

‘basal’ piece of algae; resting on the sand near the ‘apical’ or ‘basal’ piece of algae; buried in the sand; moving along the sides of the aquaria; or resting on the stone.

We conducted the activity measurements over two days for each individual, totalling 15 observations per individual during the day and 15 during the night (30 observations per individual). Individual activity was quantified as the number of movements (changes of location) that the isopod made over the 30 observations (mean 2 ± 2 movements, minimum 0 movements, and maximum 13 movements). Previously, we demonstrated that activity is a personality trait certain time periods and between situations, so we did not measure consistency of activity directly here (see Yli-Renko et al., 2015).

2.4. Predation experiment

After individual activity was quantified, we divided the isopods into three personality classes based on their activity level (low, 0–1; middle, 2–3; high, 4–13 movements per 30 observations). We used 264 individuals altogether; 119 low-active, 82 medium-active and 66 high-active. From these we created 14 groups consisting of isopods with distinct morphology in order to recognise the isopods individually after the experiment. In each group we had 18–20 isopods, roughly 50% males and 50% females. In each group, we successfully aimed for even distribution of different personality classes for both sexes as we did not find any personality differences between aquaria for either sex (GLMM females: $F_{13,110} = 0.46$, $p = 0.94$; males: $F_{13,111} = 0.31$, $p = 0.99$). As mentioned before, we based the re-identification of individuals on their sex, colour, and weight. Besides the colour-coding and information on sex and weight, we used photographs to re-identify the individuals.

To perform the predation experiment, we placed the 14 groups of isopods into 14 experimental aquaria (w: 100 cm, d: 30 cm, h: 47 cm), each filled to 40 cm depth with aerated standing brackish water and sand on the bottom. In our experimental aquaria, we created two visually different environments containing either *F. vesiculosus* (7 aquaria) or *Z. marina* (7 aquaria) to mimic two visually different predatory regimes and study whether predation is habitat-specific. We attached the vegetation to small stones with rubber bands and buried the stones under the sand.

We used European perch (*P. fluviatilis*), a common predator of *I. balthica*, that hunts visually in littoral environments in the Northern Baltic Sea. We caught 42 fish (mean size 60 g \pm 17 g) with fish traps and nets in the vicinity of the Archipelago Research Institute, immediately transported them into the laboratory in pails, and maintained them in four uniform-condition aquaria (volume of 150–350 l, 8–12 in each) for five days. Prior to the experiment, we fed the fish with gammarids.

For the experiment, we placed three fish in each experimental aquarium (without isopods) and allowed them to habituate for a couple of days before the experiment. Fish were not fed during the habituation period. After the habituation period, we removed the fish and added the isopods to the aquaria (one group of 18–19 isopods in each aquaria). Once the isopods got situated on alga (~30 min), we re-introduced the perch to the aquaria and started the experiment.

We observed the survival by removing the fish and vegetation from the aquaria and carefully counting and identifying the remaining isopods. We terminated the experiment for each aquaria when at least a third of the isopods had been consumed. If less than a third of the isopods were consumed, we continued the experiment and observed the aquaria again in the next trial. We first observed the survival three days after the beginning of the experiment, and then three days from this. As the predation was low, we lengthened the time period between observations first to four days (third check-up) and then to eight days (fourth check-up). Two aquaria were terminated after 12 days and 12 aquaria after 20 days. The set-up was designed to study the variation in the final outcome, and thus, in the later analyses we used the survival of each individual through the whole experiment as a response variable.

After the experiment, we released the fish and the surviving isopods back to the sea.

2.5. Data analysis

To compare survival probability within the personality classes and sexes in the two environments, we constructed a generalised linear mixed model (SAS Enterprise Guide 6.1, Cary, NC, USA) with binomial error distribution (alive-dead) and logit link-function. During the predation experiment, we found 11 dead isopods at the bottom of the experimental aquaria, and these were excluded from the analysis. As the individual survival probability within the same aquarium was not independent, we specified the aquarium as a random effect. We fit personality class, sex and aquarium habitat type (*F. vesiculosus* or *Z. marina*) as fixed factors and included all their interactions in the model. We tested our hypothesis that personality-dependent predation was sex-specific by including sex*personality class interaction. Similarly, the hypothesis of habitat-specific predation was studied from the by including a habitat type*personality class interaction in the model.

We also included body size (weight) as a covariate and tested the independence of the covariate and fixed factors by adding colour morph as a fixed factor, to control for their potential effects on predation. We included interactions between personality class, sex and body size to test the independence of the covariate and fixed factors (personality class*body size, sex*body size and, and personality class*sex*body size). However, we did not include colour morph in interactions as the number of replicates was not sufficient to estimate interactions (in the first place, colours were measured for identification purposes). Also as we selected individuals for identification purposes we could not control original home habitat, and this was not included the model (for example certain morphs occur mainly in *Z. marina* habitats).

We used AIC values to select the best-fit model and adjusted degrees of freedom with the Kenward-Rogers method. The final model consisted of factors that had a positive or neutral effect on model stability according to the AIC values (Table 1). The only significant interaction included personality class, sex and body size as a covariate, and thus, pairwise comparison between sex and personality class had to be done separately for small- (20 mg), medium- (40 mg) and large-sized (60 mg) individuals. We chose the covariate values based a size distribution of females and males (Fig. 1). Note that isopods are size-dimorphic, and thus, the size distribution do not completely overlap.

To assess the fit of the data to the model, we estimated residual overdispersion using the ratio of Pearson's Chi-Square to the degrees of freedom, which was 1.06. The ratio close to 1 indicates that the variability has been properly modelled and that there is no residual overdispersion. We used a non-parametric Spearman's rank correlation to study the relationship between individual body size and survival.

3. Results

Survival varied between individuals in a complicated interaction

Table 1
Final model from the GLMM analyses for isopods survival probability in predation experiment.

Effect	Num DF	Den DF	F Value	Pr > F
sex	1	233	0.02	0.88
personality class	2	233	0.37	0.69
weight	1	233	0.92	0.34
habitat	1	233	0.48	0.50
colour morph	3	233	0.82	0.50
sex*personality class	2	233	4.39	0.01
habitat*personality class	2	233	0.07	0.94
sex*weight	1	233	1.06	0.31
weight*personality class	2	233	1.21	0.30
weight*sex*personality class	2	233	3.78	0.02

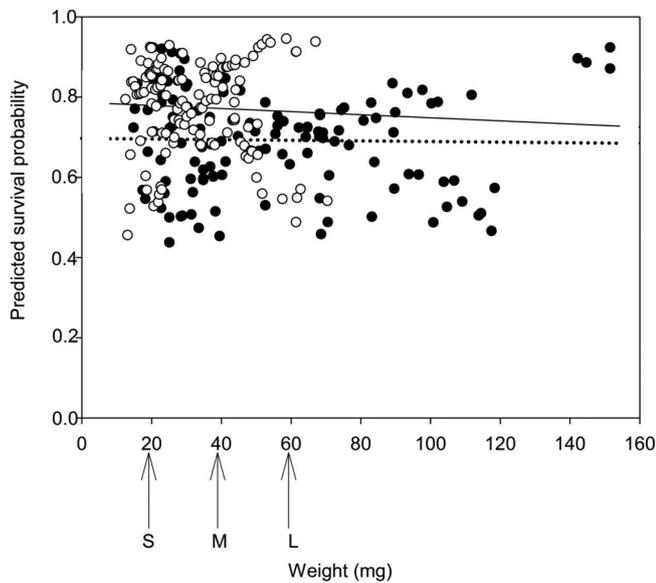


Fig. 1. Model-predicted survival with respect to isopod body weight in females and males. White circles present females (solid line) and black circles males (dotted line). Arrows indicate body sizes where pairwise comparisons were estimated (S = 20 mg, M = 40 mg and L = 60 mg).

between personality class, sex and body size. We estimated sex differences in survival probability by dividing data in personality classes (low-active, middle-active and high-active) and comparing survival in three different covariate values (body size: small-, medium-, large-sized individuals, Fig. 1).

When focusing on one personality class at the time, the size affected the survival differently in females and males (Fig. 2 a–c). Pairwise comparison between personality class*sex*body size interaction revealed indication of sex-differences in survival in high-active personality class for all sizes of individuals, especially in the medium-sized group (note that p-value of 0.06 for large sized isopods is treated as significant as this effect is biologically meaningful) (Fig. 2 a, Table 2). There were no sex-differences in any sized individuals in middle-active (Fig. 2 b, Table 2) or low-active personality classes (Fig. 2 c, Table 2).

We studied the same three-way interaction by comparing gradients from Spearman's rank correlations. Individual size affected the survival differently in females and males, but this depended on the personality class. Survival was similar for all high-active males (Spearman rank correlation: $r_s = 0.24$, $n = 29$, $p = 0.22$, Fig. 2 a). Instead, amongst high-active females larger individuals survived better than smaller ones ($r_s = 0.61$, $n = 37$, $p < 0.0001$, Fig. 2 a). Additionally, middle-active larger females survived better than middle-active smaller females ($r_s = 0.92$, $n = 37$, $p < 0.0001$, Fig. 2 b). In middle-active males, however, larger males had decreased survival compared to smaller males ($r_s = -0.90$, $n = 40$, $p < 0.0001$, Fig. 2 b). In low-active personality class, larger males had better survival than smaller males ($r_s = 0.50$, $n = 58$, $p < 0.0001$, Fig. 2c), whereas in females the larger individuals had lower survival than smaller individuals ($r_s = -0.91$, $n = 50$, $p < 0.001$, Fig. 2 c).

The personality class*sex*body weight interaction could also be studied by focusing on within-sex variation. In males (Fig. 3a), the larger individuals survived better in low-active personality class (Spearman rank correlation: $r_s = 0.50$, $n = 58$, $p < 0.0001$), but smaller individuals survived in middle-active personality class ($r_s = -0.88$, $n = 40$, $p < 0.0001$). However, the size did not affect the male survival in high-active personality class ($r_s = 0.19$, $n = 29$, $p = 0.32$). In females (Fig. 3b), the larger individuals had lower survival in low-active personality class ($r_s = -0.66$, $n = 54$, $p < 0.001$), but survival was higher for larger individuals in middle-active ($r_s = 0.90$, $n = 39$, $p < 0.0001$) and high-active ($r_s = 0.59$, $n = 37$,

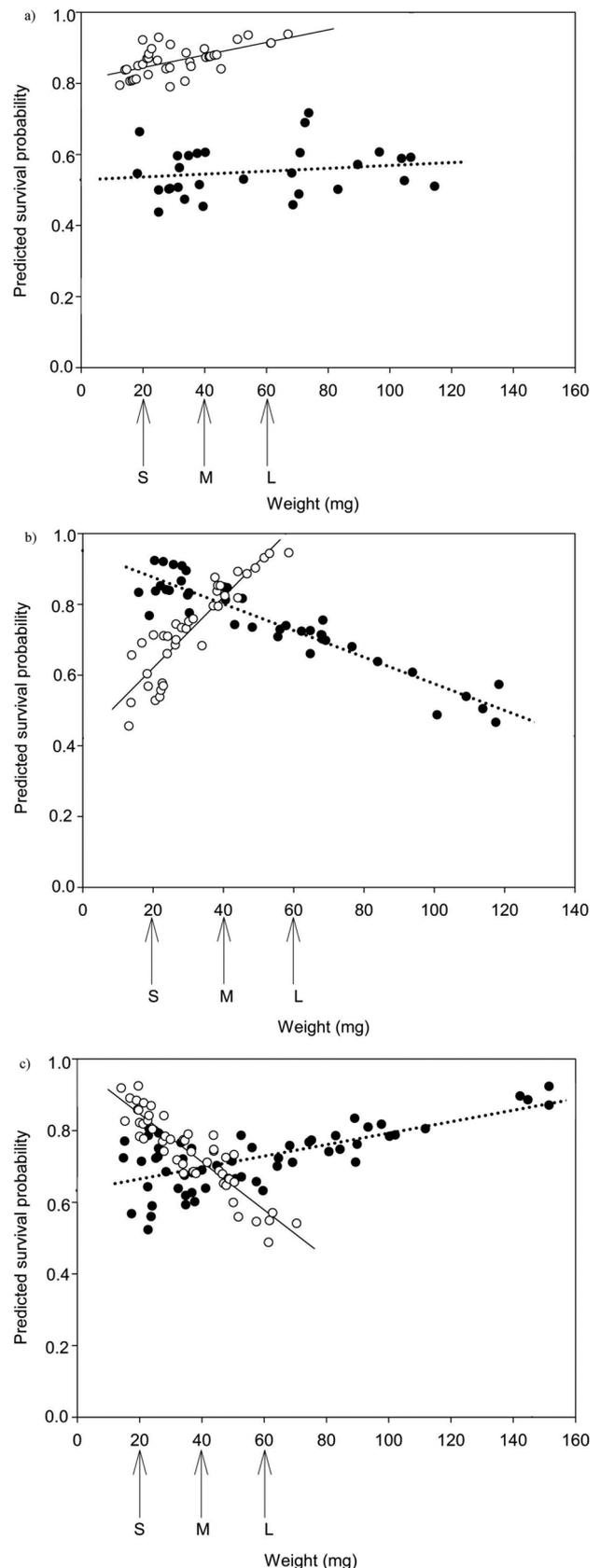


Fig. 2. a–c). Model-predicted survival with respect to isopod body weight in (a) high-active, (b) middle-active and (c) low-active personality classes. White circles present females (solid line) and black circles males (dotted line). Arrows indicate body sizes where pairwise comparisons were estimated (S = 20 mg, M = 40 mg and L = 60 mg).

Table 2

Pairwise comparison for significant personality class*sex*body size –interaction. We contrasted sexes and activity classes only at the covariate values 20 mg, 40 mg, 60 mg.

Small-sized (20 mg)		DF	t Value	Pr > t
High-active females	High-active males	233	0.0412	0.04
Middle-active females	Middle-active males	233	-1.76	0.08
Low-active females	Low-active males	233	1.67	0.10
Medium-sized (40 mg)		DF	t Value	Pr > t
High-active females	High-active males	233	2.66	0.0084
Middle-active females	Middle-active males	233	0.50	0.62
Low-active females	Low-active males	233	0.80	0.42
Large-sized (60 mg)		DF	t Value	Pr > t
High-active females	High-active males	233	1.84	0.06
Middle-active females	Middle-active males	233	1.55	0.12
Low-active females	Low-active males	233	-0.63	0.52

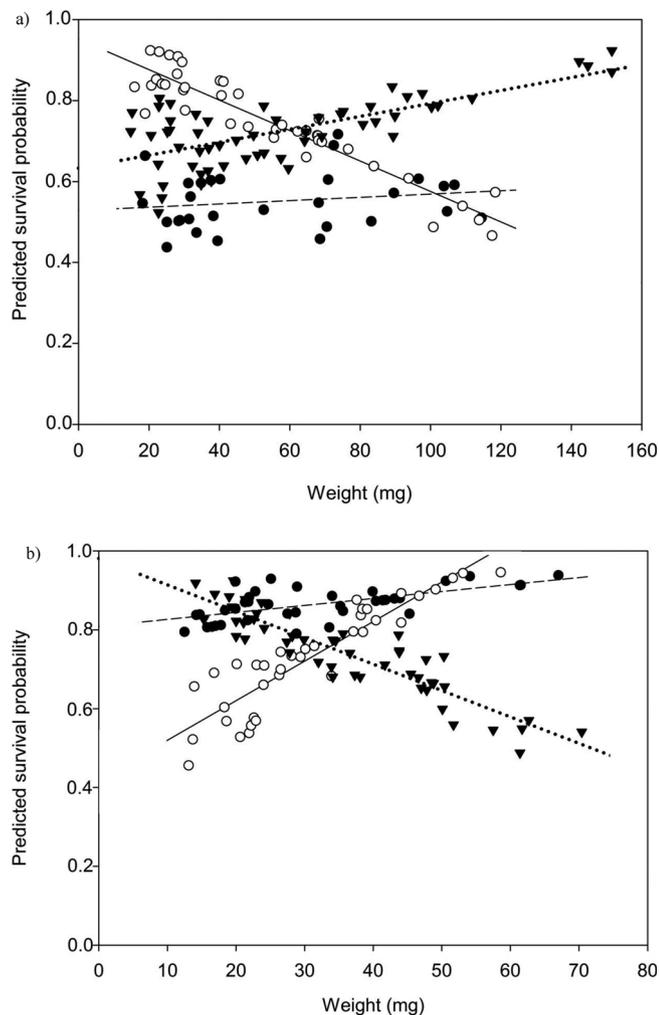


Fig. 3. Model-predicted survival with respect to body weight separately for males (a) and females (b). Black circles present high-active individuals (slashed line), white circles present middle-active individuals (solid line) and black triangles present low-active individuals (dotted line).

$p = 0.0001$) personality classes.

Survival of the sexes or personality classes did not differ between habitats. As we did not include isopods original home habitat into model we cannot account for background experience with habitat type. Colour morph did not affect survival of the isopods indicating that the allocation of individuals to the experimental aquariums based on identification did not influence the results (Table 2).

4. Discussion

We found that survival varied between individuals in a complicated interaction between personality class, sex and body size. Predation pressure contributes differently to survival in females and males, as survival of males was lower than in females in the high-active personality class. Moreover, survival under predation was linked to body size differently in females and males. The larger size was beneficial for low-active males and middle- and high-active females but low-active females and middle-active males benefit for smaller size. Size did not affect survival in high-active males. The relationship between predation and personality is well documented (e.g. Réale and Festa-Bianchet, 2003; Dingemans and Réale, 2005; Smith and Blumstein, 2010), yet studies focusing on sex-specific predation on personality types are still rare. Thus, the link between sex and personality in natural prey-predator interactions is less explored in animal personality studies.

In general, isopods are known to have sex-based differences in activity levels (Jormalainen and Tuomi, 1989; Vesakoski et al., 2008). Adult females and males also differ in their habitat choices as the sexes prefer different microhabitats with females found more often at the lower parts of *F. vesiculosus* thalli than males (Merilaita and Jormalainen, 2000), probably due to the females' stronger anti-predator adaptations as in lower parts females are less exposed to predators. Females are less active during day-time when visually hunting predators are active (Jormalainen and Tuomi, 1989; Vesakoski et al., 2008) and less active during day-time in the presence of a predator cue (Yli-Renko et al., 2015). Due to these sex-based differences in behaviour, the selection pressures caused by predation are likely to vary between sexes, and this may explain why selection acted against active males. For example, as females prefer more sheltered parts of host algae, being active might not affect survival as much as males that prefer more visible parts of the host algae. This can explain why survival was low for all sized high-active male individuals compared to females. Additionally, earlier studies have reported relation between personality and predation (Réale and Festa-Bianchet, 2003; Bell, 2005; Dingemans et al., 2007; Brydges et al., 2008; Smith and Blumstein, 2010; Edenbrow and Croft, 2013). These studies did not especially consider the hypothesis of sex-specific predation maintaining personality variation in a population, but show that predation is likely to create selection pressures on personalities. Our results combined with the evidence from previous studies show that predation pressure is one of the main driving forces behind selection patterns of personality traits.

It has been hypothesised that in isopods active males have higher mating success than non-active males (Jormalainen and Tuomi, 1989; Vesakoski et al., 2008) as in this species male fitness depends on its ability to locate females to mate with, whereas in females fitness is more related to egg production (Tuomi et al., 1988). Activity is also beneficial for finding food, which allows for faster growth. Fast growth is considered as a good proxy for fitness in isopods as their body size is correlated with fertility and reproductive success both in males and females (Jormalainen et al., 1992; Jormalainen et al., 1994; Jormalainen and Merilaita, 1995; Hemmi and Jormalainen, 2004). A previous study with personality of isopods has found activity to be harmful for isopods as winter mortality in laboratory settings was higher for high-active individuals than low-active and the pattern was similar for both sexes (Yli-Renko et al., 2015). In our present study, we found that survival probability under predation was linked to body size differently in females and males as low-active larger male isopods survived better than low-active smaller males and the pattern was the opposite for females. Moreover, in high-active females larger individuals survived better than smaller individuals, but when male isopods were high-active, size had no effect on their survival. In males, the optimal strategy for mating success would be high activity and large size (Tuomi et al., 1988; Jormalainen and Tuomi, 1989; Vesakoski et al., 2008). Our results combined with previous knowledge of winter

survival of high-active individuals without predation (Yli-Renko et al., 2015) predicts low reproductive success for active males as they died before the breeding season. In females, breeding success is more related to body size than activity (Tuomi et al., 1988; Hemmi and Jormalainen, 2004), and the optimal life strategy for females would be low-activity (winter survival) and larger size (fecundity). However, based on our present results, female survival probability under predation in low-active personality class is lower for larger than smaller females. Thus, selection for fecundity is expressed inversely to survival, creating trade-offs between finding mates and food, and exposure to predation and winter mortality supporting the idea by Stamps (2007) and Wolf et al. (2007) that the evolution of animal personality is probably a compromise between counteracting selective forces creating life-history trade-offs between reproduction and predation.

Our results suggest that there are intersexual life-history differences (survival) in isopods that could lead to personality variation (measured as a consistency of behaviour) between sexes, as hypothesised in Schurch and Heg (2010). Although Schuett et al. (2010) have reviewed more consistent behaviour for males, these sex-differences in personality (activity) have not been found in *I. balthica* (Yli-Renko et al., 2015). Our present study shows that both sexes have an optimal life strategy for activity. Because selection favours a certain personality type for females and males, predation can encourage life-history differences between sexes. On account of this, sex-dimorphism in personality (consistency of activity levels) is prevented by predation, i.e. under predation both sexes have optimal activity-level although this differs between sexes. This results in consistent activity levels (personality) for both sexes.

We also studied the hypothesis that variation in personality would be produced by varying predation pressures in different habitats. The survival probability of the individuals was similar in the two experimental environments, which suggested that predation by *P. fluviatilis* would not select for different personalities in these two different physical environments. Some earlier studies indicate that environment could mediate predation on personalities. For example, in three-spined sticklebacks (*Gasterosteus aculeatus*), boldness varied between fish from a river and from a pond, with river fish less bold than pond fish. This variation was likely caused by both predation pressure and habitat stability as ponds were more stable habitat compared to rivers (Brydges et al., 2008). It remains possible that in our study the habitats created in aquaria did not mimic nature adequately. We need more studies on population-divergence in personalities combined with experimental studies to test the mechanism of selection to assess the degree of the environment-specific predation pressures.

Here we provide experimental evidence for the hypothesis that life-history trade-offs maintain consistent behavioural difference between individuals in activity. We found that predation pressure contributes differently to survival in females and males, as male survival was lower than female survival in the high-active personality class. Moreover, predation was linked to body size differently in females and males. This, however, depended on personality class, as the larger size was advantageous for low-active males and middle- and high-active females. Instead, smaller size was advantageous for low-active females and middle-active males. Size did not affect survival in high-active males. Our results suggest that predation can encourage life-history differences between sexes leading to different optimal life-history strategies and also maintains consistent activity for both sexes.

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