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Reference:

Vanden Broecke Bram, Sluydts Vincent, Mariën Joachim, Sabuni Christopher Andrew, Massawe Apia W., Matthysen Erik, Leirs Herwig.- The effects of personality on survival and trappability in a wild mouse during a population cycle
Oecologia - ISSN 0029-8549 - 195:4(2021), p. 901-913
Full text (Publisher's DOI): https://doi.org/10.1007/S00442-021-04897-9
To cite this reference: https://hdl.handle.net/10067/1774040151162165141

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Author contributions: BVB, JM, AM, EM & HL conceived and designed the study. BVB collected the data with support of JM, CAS and AM. BVB and VS performed the data analysis with input from JM, EM and HL. The first draft was written by BVB and all authors contributed substantially to revisions.

ABSTRACT

The pace-of-life syndrome (POLS) theory provides an evolutionary explanation for the existence of consistent among-individual variation in behaviour, or animal personality. Herein, individuals with a fast lifestyle are considered to be bolder and should take more risks resulting in a lower life expectancy compared to shyer individuals with a slower lifestyle. However, this assumption depends on the levels of intra-specific competition that the individuals experience which has rarely been tested in species that experience large changes in competition on a very short time scale. We used the multimammate mice (*Mastomys natalensis*) as a model system to study the POLS assumption by investigating the effects of two personality traits (exploration and stress-sensitivity) on survival, maturation (a proxy for reproductive investment) and recapture probability during one population cycle ($N_{individuals} = 201$). Such a cycle consists of two phases in which the levels of intra-specific competition varies drastically. We found that only one personality trait, namely stress-sensitivity, had a negative effect on both survival and recapture probability but none of them affected maturation. This suggests that less stress-sensitive individuals take more risks in the wild and have a higher survival probability compared to high stress-sensitive individuals. However, the effect of personality on survival was only present during the population decrease phase, when the levels of intra-specific competition are high due to a scarcity of food. This suggests that seasonal changes in competition might be important in the evolution and maintenance of animal personalities in species whose population dynamics have a clear seasonal component.

Keywords: exploration, stress-sensitivity, density, pace-of-life syndrome, capture-mark recapture, *Mastomys natalensis*

INTRODUCTION

Consistent behavioural variation among individuals, or animal personality, has been found in a wide variety of species (Gosling 2001; Réale et al. 2007; Carere and Maestripieri 2013), affecting fitness (Smith and Blumstein 2008; Moiron et al. 2020), cognition (Dougherty and Guillette 2018), mate choice (Schuett et al. 2010; Pogány et al. 2018) and parasite and virus transmission (Boyer et al. 2010; Barber and Dingemanse 2010; Vanden Broecke et al. 2019). However, the evolutionary mechanisms responsible for the existence and maintenance of this phenotypic variation is still not well understood. One potential evolutionary explanation is given by the pace-of-life syndrome (POLS) theory, which integrates behaviour, life history and physiology into one framework. This theory assumes that each individual faces a trade-off in resource allocation between current reproduction and future survival resulting in fast versus slow lifestyles (Réale et al. 2010; Dammhahn et al. 2018; Mathot and Frankenhuis 2018). Individuals with a fast lifestyle are thought to invest more of their energy into current reproduction instead of survival and therefore mature faster but die sooner compared to individuals with a slow lifestyle. In order to sustain this fast lifestyle, they are expected to be consistently more explorative, active and bolder compared to slower individuals. These slower individuals should, on its turn, invest more of their energy into future reproduction and survival and therefore need to be shyer, less explorative and less active (Réale et al. 2010). Nevertheless, empirical evidence is equivocal since the effects of personality on survival might depend on the individual's environment (Royauté et al. 2018; Montiglio et al. 2018; Santicchia et al. 2018). Indeed, a recent meta-analysis has shown that survival is associated with personality in wild populations but not in the laboratory, potentially due to different selection pressures caused by the absence of predation and higher levels of food availability in the lab compared to the wild (Moiron et al. 2020).

However, selection pressures may also vary within one specific environment, due to changes in density. Indeed, population density is being proposed as an important factor within the POLS theory, since it may lead to density-dependent variation in selection pressures (Araya-Ajoy et al. 2018; Montiglio et al. 2018; Wright et al. 2019; Dhellemmes et al. 2020). For instance, Wright et al., (2019) suggested that changes in intra-specific competition, due to temporal variation in population density, might result in fluctuating density-dependent selection which generates variation in fast versus slow life histories within populations. According to this theory, individuals with a fast lifestyle should perform better when population densities are low, which is accompanied with lower levels of intra-specific competition compared to populations with higher densities. Those high density populations are, in turn, more suited for individuals with a slower lifestyle, since they are expected to experience fewer negative effects of intra-specific competition due to their low levels of aggressiveness, activity and metabolism (Réale et al. 2010). This among individual variation in tolerance against competition may eventually lead to differences in survival between individuals with a fast versus slow lifestyle, depending on the population density. Herein it is expected that the survival probability of individuals with a fast lifestyle is negatively correlated with population density and this has been confirmed in several species. Survival of fast exploring great tits (*Parus major*), for instance, decreases when density goes up while this is reversed for slow explorers (Nicolaus et al. 2016). Similar results have been found in the common lizard (*Zootoca vivipara*) where the survival increased for social and less active individuals at low densities (Le Galliard et al. 2015).

These effects would then eventually lead to variation in the composition of behavioural types within the population, where individuals with a fast lifestyle, who are bold, aggressive, active and highly explorative would occur more frequently at lower densities compared to shyer, less active and less aggressive individuals with a slow lifestyle. However, these predictions have rarely been tested in species who experience large fluctuations in population size on a very short timescale within their lifespan (Andreassen et al. 2020), and with contrasting results.

Common voles (*Microtus arvalis*), for instance, which were captured just before the breeding season, when densities are low, were significantly bolder compared to individuals caught during high density phases (Eccard and Herde 2013). Potentially because boldness would increase the individuals' reproductive success at the expense of their survival, suggesting that these bolder individuals exhibit a fast lifestyle. While this pattern corresponds with the proposed predictions, the opposite has been observed in other vole species. Krebs (1970), for example, found that male prairie (*M. ochrogaster*) and meadow voles (*M. pennsylvaticus*) were significantly more aggressive during periods of high density, when levels of intra-specific competition are high (Getz et al. 2001). Similar results have been found in the multimammate mice (*Mastomys natalensis*) where more explorative and stress-sensitive individuals were caught at higher densities (Vanden Broecke et al. 2019).

In this study, we used the multimammate mouse (*M. natalensis*) to test how seasonal variation in intra-specific competition influences the effect of personality on survival and maturation allowing us to test the POLS predictions during two different competitive environments. *M. natalensis*, a murid rodent pest species in sub-Saharan Africa, is a perfect candidate model system to study these predictions since they experience strong seasonal fluctuations in density (from 20 to 500 individuals) within one year which are accompanied by drastic changes in intra-specific competition due to variation in resource availability (Leirs et al. 1994, 1997; Sluydts et al. 2007). This is because their reproductive cycle is strongly correlated with seasonal rainfall patterns which affect food availability and results in yearly population cycles (Leirs et al. 1994, 1997; Sluydts et al. 2007). These cycles have two distinct phases (Figure 1) with different levels of intra-specific competition. The first phase is the population increase phase, which starts immediately after the rainy season and initiates the main breeding season (Leirs et al. 1994, 1997; Sluydts et al. 2007). During this period, food is abundantly available resulting in low levels of intra-specific competition (Leirs et al. 1990; Borremans et al. 2014). The second phase is the population decrease phase and starts at the end of the dry season when food becomes more limited. This leads to an increase in mortality and higher levels of intra-specific competition for food which eventually leads to a population crash (Leirs et al. 1990; Sluydts et al. 2007; Myers 2018).

We used capture mark-recapture data to investigate the effect of two personality traits (see below) on the individual's survival, maturation (which can be seen as a proxy for reproductive investment) and recapture probability during one population cycle. The latter is commonly referred to as trappability (i.e. the probability that an individual is recaptured) and is being used as a common field measurement for boldness since it represents risk taking towards a novel object in their natural environment (Garamszegi et al. 2009; Boyer et al. 2010; Carter et al. 2012; Montiglio et al. 2012; Santicchia et al. 2018; but see: Brehm and Mortelliti 2018; Jolly et al. 2019; Santicchia et al. 2020). Studying trappability in combination with a classic hole-board test allows us to determine if the two personality traitsy, measured in standardized lab conditions, are ecologically relevant in natural conditions (Carter et al. 2013; Royauté et al. 2018) and therefore linked to different lifestyles. Two personality axes have been described in *M. natalensis* using a hole-board test (Vanden Broecke et al. 2019), but it is currently unclear if they affect survival, maturation or trappability. The first one is an exploration-activity axis (referred to as exploration) where highly explorative individuals are more active and explore the blind holes more frequently compared to less explorative individuals (Vanden Broecke et al. 2019). The second personality axis is a grooming-jumping axis (referred to as stress-sensitivity) where less stress-sensitive individuals spent more time grooming themselves (following the cephalocaudal rule, which occurs in low stress environments Smolinsky et al. 2009) and jumped less frequently during the behavioural observation compared to high stress-sensitive individuals (Vanden Broecke et al. 2019, 2020).

We predicted a positive correlation between recapture probability and exploration but not with stress-sensitivity, since only exploration has been found to covary with trappability in several species (Garamszegi et al. 2009; Boyer et al. 2010; Montiglio et al. 2012). This prediction implies that highly explorative individuals would take more risks in the wild and therefore exhibit a faster lifestyle compared to less explorative and more cautious individuals who then exhibit a slower lifestyle. We then predicted that these risky and highly explorative individuals, with a fast lifestyle, would invest more energy into their reproductive success instead of survival. They should therefore mature faster but exhibit a lower life expectancy compared to individual with a slow lifestyle, since the central paradigm within the POLS theory is the trade-off between current reproduction and future survival (Mathot and Frankenhuis 2018). However, the effect of personality on survival may depend on the level of competition among individuals and is therefore expected to vary within one population cycle. During the population increase phase, we predicted no differences in survival between individuals with a fast or slow lifestyle, since food is abundant resulting in low levels of intra-specific competition (Leirs et al. 1990; Borremans et al. 2014). However, food becomes limited during the population decrease phase which results in an increased competition among individuals. During this period, a negative correlation between survival and exploration behaviour is expected since these individuals, with a fast lifestyle, should be less resistant to these high levels of intra-specific competition (Wright et al. 2019). The strength of this negative association between exploration and survival might differ between the two sexes due to differences in reproductive success and mating strategy (Hämäläinen et al. 2018). Indeed, reproductive success varies strongly between males and females since almost all females reproduce during their lifetime (Sluydts et al. 2009) but only a small percentage of the males (17-40%) father all offspring (Kennis et al. 2008). We therefore predict that the trade-off between current reproduction and future survival might be more pronounced in males than females resulting in a stronger effect of exploration on survival in males, during the population decrease phase, compared to females.

MATERIAL AND METHODS

Study species

Mastomys natalensis is one of the most common indigenous rodents in sub-Saharan Africa where it is known to be an important agricultural pest species (Leirs et al. 1994), host for several zoonotic pathogens (Frame et al. 1970; Ziwa et al. 2013) and they have an opportunistic and generalist diet (Leirs et al. 1994; Odhiambo et al. 2008; Mulungu et al. 2011, 2014; Mlyashimbi et al. 2018). Two personality traits have been found in this species: exploration and stress-sensitivity (Vanden Broecke et al. 2018, 2019, 2020).

Their reproductive cycle is strongly correlated with seasonal rainfall patterns which affect food availability and lead to strong seasonal and annual fluctuations in density (Leirs et al. 1994, 1997; Sluydts et al. 2007). Populations in East Africa, for instance, fluctuate from 20 to 500 individuals per hectare in a couple of months (Leirs et al. 1997; Sluydts et al. 2007). However, most individuals experience only one cycle during their lifetime since only a few animals live longer than 300 days (Leirs et al. 1993). The breeding season starts in May immediately after the first rainfall (March – Jun) and lasts until October. The non-breeding season starts after this period where the animals enter a growth stop which lasts until April (Leirs et al. 1990, 1994). The analysis of movement patterns during a long-term field study has shown that home ranges overlap increases during periods of high resource availability indicating a low level of territoriality and reduced spatial activity (Borremans et al. 2014), which may support the scramble mate competition, where males roam around to find females (Kennis et al. 2008).

Experimental setup

In order to estimate the effects of personality on survival, maturation and recapture probability, we performed a semi-wild experiment at the Sokoine University of Agriculture (SUA), Morogoro, Tanzania, using three 0.5ha (70 x 70 m) enclosed fields (named A, B and C), in which we released rodents that were captured in three different areas elsewhere on the campus (see Vanden Broecke et al. (2019) for a more detailed description about the experimental setup). The habitat inside the enclosures consisted of a mix of grasses and shrubs, similar to their natural habitat, providing natural cover against predators and weather. The enclosures were constructed of galvanized steel, 100 cm above and 70 cm below the ground which prevented them from escaping out of the enclosures (Vanden Broecke et al. 2019). Being inside these enclosures has potentially little effect on the individuals' spatial behaviour, since these enclosures were almost 10 times larger than the mean home range size of *M. natalensis* (Borremans et al. 2014).

We implemented capture–mark–recapture trapping with a robust design (Pollock 1982) where we trapped for 3 consecutive nights every 2 weeks in each enclosure from June 2017 until March 2018 (which follows one population cycle, Figure 1). We placed 100 Sherman LFA live traps (Sherman Live Trap Co., Tallahassee, FL) within each enclosure in the evening (around 16:00), using a mix of peanut butter and maize flour as bait and checked them in the early morning (5:00). We recorded the weight, sex and reproductive age following Leirs et al. (1994). We considered mice to be juveniles if no signs of sexual maturity could be observed (scrotal testes in males; perforated vagina or pregnancy in females). Individuals were uniquely marked using toe clipping. We chose to use this procedure over other less-invasive procedures since we needed lifelong marks which were easily recognizable during the fieldwork. Additionally, it has been shown, using a 17 year capture-mark-recapture dataset of wild caught *M. natalensis* in Tanzania, that toe clipping has no effect on the individuals body weight, survival and movement (Borremans et al. 2015). The individuals were held for a maximum of 5 hours and were released at the point of capture at the end of the experimental procedure. We conducted a total of 12, 16 and 14 trapping session for field A, B and C, respectively. Each trapping session was separated by two weeks except for three sessions where the time between subsequent sessions was one month and one with three weeks. These unequal time intervals were taken into account in the models.

Behavioural trials were conducted from June until October 2017 at the site of capture before blood sampling (~70 µL taken from the retro-orbital sinus and preserved on pre-punched filter paper; see Vanden Broecke et al. (2019) for a more detailed description) and toe clipping in order to minimize any stress effects. The individuals' behaviour was recorded inside a hole-board test once per trapping session, when they were trapped for the first time within that session. The hole-board test is derived from the open field test with holes in the floor to measure exploration independently of activity (File and Wardill 1975; Martin and Réale 2008). The box (75x55x90 cm; LxWxH, respectively) was constructed out of strong white plastic with six blind holes in the bottom (Ø: 3.5 cm; depth: 6 cm) each spaced 19 cm apart. The box was closed off with a lid with a small hole for the infrared camera. Behavioural recordings started when the individual was inside the box and the lid was closed and lasted for 10 minutes. During this period, we measured five different behaviours: activity (the number of times an individual crossed one of the 12 squares), the number of times they sniffed a hole, number of head dips (when both eyes and ears disappear into one of the blind holes; File and Wardill 1975; Martin and Réale 2008), the time they spent grooming and the number of jumps. A more detailed description can be found in Vanden Broecke et al. (2019). The box was cleaned with 70% ethanol to remove animal scent and dirt.

All experimental procedures were approves by the University of Antwerp Ethical Committee for Animal Experimentation (2016-63) and adhered to the EEC Council Directive 2010/63/EU and followed the Animal Ethics guidelines of the Research Policy of Sokoine University of Agriculture.

Statistical analysis

Data selection

The main question of this study was to investigate the effect of personality on survival, maturation and recapture probability. Therefore, we could only include individuals in the capture-mark-recapture analysis (CMR) for which we had information about their personality and whose behaviour was thus recorded at least twice. We conducted a total of 652 behavioural recordings of 201 unique individuals which were recorded on average three times (range = 2 - 8 observations) with on average 19 days between subsequent recordings (range = 12 – 71 days). The CMR dataset consisted out of 1396 captures (see Table 1 in the supplementary material for a detailed summary of the sample size), where each individual was caught on average 6.9 times (range = 2 – 30). The individuals that were used in this study are the same individuals as studied in Vanden Broecke et al. (2019).

Personality assessment

We followed the behavioural analysis of Vanden Broecke et al. (2019), since the data from this study was derived from the same experiment. They used a principal component analysis (PCA) on all the behaviours expressed in the hole-board test to reduce the amount of variables, which resulted in two axes: exploration and stress-sensitivity. We decided to use these components in this study as well, since it would allow us to compare our results with previous work of animal personality in *M. natalensis* (Vanden Broecke et al. 2018, 2019, 2020).

However, the software that we used to conduct the CMR analysis could only use a single personality value per individual for exploration and stress-sensitivity, instead of the multiple measurements that were taken per individual for both personality traits. We therefore decided to use the best linear unbiased predictors (BLUPs) from the final models described in Vanden Broecke et al. (2019). The linear mixed model with exploration as response variable included the individual’s reproductive age, sex, antibody presence against the Morogoro virus, test sequence, density (centred both between as within individuals; van de Pol and Wright 2009) as fixed effects. The model with stress-sensitivity as response variable included the individuals’ reproductive age, test sequence and density (centred within individuals) as fixed effects. The individuals’ identity, the enclosure in which the individual was trapped in and the place where the individual originated from were included as random effects in both models. A more detailed description of these models can be found in Vanden Broecke et al. (2019). BLUPs are standardized to a mean of zero and provide estimates of the random effects (ID) independent of the other terms within the model (Kruuk 2004; Martin and Réale 2008). They are less sensitive to extreme values within the data and are a more appropriate measure for personality scores than the mean of all measurements from one individual (Pinheiro and Bates 2000). The use of BLUPS in subsequent analysis has been criticized since it does not account for the uncertainty around the BLUP estimates (Hadfield et al. 2010; Houslay and Wilson 2017). An alternative is to simulate 1000 BLUPs for each individual using the sim function in the arm package (Gelman et al. 2020) and use the mean BLUP of these 1000 simulated estimates in further analysis, as proposed by Dingemanse et al. (2020). These simulated BLUPS were, however, exactly the same as those derived from the linear mixed models for both exploration ($R^2 = 1$) as for stress-sensitivity ($R^2 = 1$). We therefore decided to continue with the BLUPS derived from the linear mixed models, instead of the simulated BLUPS.

Goodness of fit

A goodness of fit (GOF) test was carried out with the program U-CARE prior to the survival analysis to evaluate potential confounding factors such as an excess of transience animals (null hypothesis is that there are no difference in the recapture probability between newly trapped and recaptured individuals) and trap-dependence (null hypothesis is that the recapture probability is affected by previous trapping experience; Pradel et al. 2003; Choquet et al. 2009a). The GOF test did not show any deviation against the assumption of transience (Test 3G.SR: see results), but we did find a strong effect of trap-dependence, where the individuals became trap happy. This means that the recapture probability of individuals that were trapped during the previous trap session was higher than those that were not trapped (Test M.ITEC: see results). We therefore had to implement the aware-unaware method, described by Pradel and Sanz-Aguilar (2012) in the models to correct for trap awareness.

Modelling

The CMR data was analysed using E-surge V2.1.4 (Choquet et al. 2009b). We used multi-event capture-recapture models to estimate the effects of the two personality traits (exploration and stress-sensitivity) on survival (ϕ), maturation (Ψ) and recapture probabilities (P). These models are an extension to classic capture-recapture models where the number of states can be greater than the number of events (Lebreton and Pradel 2002; Pradel 2005). We included three events (captured as juvenile/adult or not captured; see matrix in the supplementary material) and five states (trap aware and unaware juvenile/adults or dead; see matrix in the supplementary material), which allowed us to incorporate detection heterogeneity into our models (Pradel and Sanz-Aguilar 2012). The use of Pollock's closed robust design during trapping allowed us to estimate survival between each trapping session, since the population is assumed to be closed (i.e. no entry or exit of individuals into the population) within each trap session and open between trapping sessions (Pollock 1982). Recapture probabilities, on the other hand, were estimated within each session.

In order to simplify the full model (containing 47 parameters), we used a modelling strategy to reduce the number of plausible models by performing a stepwise model selection procedure (following: Sluydts et al. 2007; Mayamba et al. 2020; Ademola et al. 2021) in an ordered fashion; first survival probability was modelled, followed by maturation rates and lastly recapture probability. In each step, we started with a full model (Table 1) which included the two personality traits and all relevant interactions (see below for a more detailed description). We then started by removing the interactions one by one until both personality traits had an additive effect. Models were ranked using the corrected Akaike's information criterion (AICc; Burnham and Anderson 2004). We then selected the model with the lowest AICc and removed both personality traits one by one until both were removed from the model. The model with the lowest AICc value (marked in bold in Table 1) was then considered to be the best fitting model within that modelling step and was used in the next modelling step. All covariates were standardised to have a mean of zero and a variance equal to one to help convergence (White and Burnham 1999).

Survival

Our measurements were taken during one population cycle (see Figure 1) which consists of two seasons: the breeding season (May-October) and the non-breeding season (November-April) which are, respectively, the increase and decrease phase of the population cycle (Figure 1). Since we are interested in the variation in survival between these two phases, we decided to estimate survival seasonally instead of a full time-dependent effect (in which survival is estimated separately between every trapping session). In the full model, survival was allowed to covary with both personality traits (exploration and stress-sensitivity) separately in both seasons. However, the effect of personality might differ between males and females and we therefore included an interaction with sex within each season. Reproductive age (juvenile or adult) was included as an additional fixed effect over the seasons, to correct for variation in survival between these two age classes (Sluydts et al. 2007, 2009). Lastly, the enclosure (A, B or C) where the individual was caught was included as additional additive fixed effect over the two seasons in order to correct for potential unaccounted variation between the three replicates. Both reproductive age and the enclosure in which the individual was trapped were never removed and were thus present in all subsequent modelling steps. Model selection started with the full model of the increase phase where we stepwise removed both personality traits (and their interaction with sex) until only the sex effect remained. We then selected the model with the lowest AICc and started reducing the full model of the decrease phase, following the same procedure. We used the same maturation (only sex) and recapture parameters in all models. The latter was allowed to differ between trap aware and unaware individuals, the three enclosures and between every trapping session (i.e. fully time dependent).

Maturation

Maturation is defined as the biweekly probability for juveniles to become adults, i.e. to become reproductive active since adults and juveniles were differentiated from each other based on signs of sexual activity. We allowed maturation rate to covary with both exploration and stress-sensitivity in the full model in order to investigate the effect of personality on the probability to become reproductive active. However, this effect might differ between males and females. We therefore included an interaction between the two personality traits with sex in the full model as well. Model reduction started by removing the interaction terms until all three terms (exploration, stress-sensitivity and sex) had an additive effect after which we removed both personality traits one by one until only the sex effect remained. We used the same recapture parameters for all models, as described above.

Recapture

Recapture probabilities were estimated within each trapping session and was estimated separately for trap aware (trapped during the previous session) and trap unaware individuals (those that were not trapped during the previous session). Both exploration and stress-sensitivity were included in the full model, allowing us to investigate the effect of personality on the recapture probability. However, this effect might differ between trap aware and unaware individuals. We therefore included an interaction between trap-awareness and personality. We included sex as an additional fixed effect in the model, since it has been shown that males and females differ in the recapture probability in *M. natalensis* (Mayamba et al. 2020). Lastly, the enclosures were included as an additional additive effect, which allowed recapture probabilities to differ among the three enclosures. The full model was fully time dependent, meaning that we allowed the recapture probability to differ between the different trapping sessions.

RESULTS

Goodness of fit

The GOF test showed no deviation against the assumption of transience (Test 3G.SR: $\chi^2 = 2.684$, df = 17, P = 1.000), which was expected since we could only use the individuals whose behaviour was recorded at least twice and thus were trapped at least two times. We did find deviation against the assumption of trap dependence (Test M.ITEC, $\chi^2 = 150.134$, df = 58, P <

0.001, animals became trap-happy), suggesting that the recapture probability of individuals that were trapped in the previous session is higher than those that were not trapped in that session, which is in line with previous studies on *M. natalensis* in Tanzania (Sluydts et al. 2007; Borremans et al. 2015; Mariën et al. 2018; Mlyashimbi et al. 2019).

Model selection

Survival

The model with the lowest AICc value during the population increase phase included only sex where the survival of females (ϕ_{female} = 0.91; 95% CI: [0.86 – 0.95]) was similar as in males (ϕ_{male} = 0.93; [0.86 – 0.96]). This model was 0.40 AICc units smaller than the next model which included sex and stress-sensitivity as additive effects (Table 1). However, the effect of stress-sensitivity on survival during the population increase phase was low (estimate = -0.18; 95% CI: [-0.45 – 0.09]) and the 95% CI overlapped with zero, suggesting that this effect was not important. We therefore decided to remove the effect of both personality traits on survival during the population increase phase in the subsequent modelling steps.

The best fitted survival model during the population decrease phase included stress-sensitivity with an interaction with sex (Table 1). However, this effect of stress-sensitivity differed between males and females (Figure 2B). While the survival of males during the decrease phase decreased strongly with stress-sensitivity (-0.56; [-1.05 – -0.07]; intercept = 0.82; [0.21 – 1.42] ; Figure 2B), it did not affect female survival (0.06; [-0.22 – 0.33]; intercept = 0.90; [0.38 – 1.42]; Figure 2B). This model was 1.60 AICc units smaller than the model which only included sex (Table 1), which indicates that both models adequately fit the data. This small difference in AICc between the two models is possibly due to the fact that stress-sensitivity had only a significant effect on survival in males.

The best fitting model also revealed, besides the effect of stress-sensitivity on survival, that juvenile survival was higher than adult during both the population increase ($\phi_{juvenile}$ = 0.97, [0.94 – 0.98]; ϕ_{adult} = 0.92, [0.89 – 0.94]) and decrease phase ($\phi_{juvenile}$ = 0.87, [0.80 – 0.92]; ϕ_{adult} = 0.71, [0.65 – 0.76]) and that there were no differences in survival between the three enclosures ($\phi_{enclosure\ A}$ = 0.87, [0.81 – 0.91]; $\phi_{enclosure\ B}$ = 0.89, [0.86 – 0.92]; $\phi_{enclosure\ C}$ = 0.87, [0.83 – 0.90]). We decided to continue with the model with the lowest AICc value for the next modelling steps, where survival was allowed to differ between the two sexes in both the population increase and decrease phase, with an additional interaction with stress-sensitivity during the population decrease phase (Table 1).

Maturation

The best fitted model contained only sex, where males matured faster (Ψ_{males} = 0.09 [0.06 – 0.13]) compared to females ($\Psi_{females}$ = 0.06 [0.04 – 0.08]). The difference in AICc with the second best fitting model was 1.08 units, which included an additional effect of stress-sensitivity. However, the 95% confidence interval of the effect of stress-sensitivity on maturation overlapped with zero (estimate = 0.13 [-0.12 – 0.38]), which suggests that this effect was not statistical significant. We therefore decided to continue with the model with the lowest AICc value, which only included sex.

Recapture

The model with the lowest AICc value (ΔAICc = -2.03 from the second best fitting model; Table 1) included trap awareness with an interaction with stress-sensitivity. This model revealed that the recapture probability of trap aware individuals was negatively correlated with stress-sensitivity (0.18; [-0.29 – -0.06]; intercept = -0.49; [-0.78 – -0.19]; Figure 3), while this effect was absent for trap unaware individuals (0.01; [-0.10 – 0.11]; intercept = -1.25; [-1.53 – -0.97]; Figure 3).

Additionally, female recapture probability was higher compared to males for both trap aware ($P_{females}$ = 0.50 [0.47 – 0.53]; P_{males} = 0.39 [0.36 – 0.43]) and trap unaware individuals ($P_{females}$ = 0.32 [0.29 – 0.35]; P_{males} = 0.23 [0.21 – 0.26]). The model also revealed that there were considerable differences in recapture probability between the three enclosures ($P_{enclosure\ A}$ = 0.29 [0.25 – 0.33]; $P_{enclosure\ B}$ = 0.36 [0.34 – 0.39]; $P_{enclosure\ C}$ = 0.42 [0.39 – 0.45]).

DISCUSSION

We have provided evidence that both survival and recapture probabilities in *M. natalensis* are personality dependent. Our results show that stress-sensitivity, a personality trait earlier described in Vanden Broecke et al. (2019), was negatively associated with both recapture probability (i.e. trappability) and male survival probability. This suggests that less stress-sensitive individuals have a higher survival probability, compared to more stress-sensitive individuals, even though they take more risks in the wild. However, the individual's personality affected survival only during the population decrease phase, when the levels of intra-specific competition are high, due to a scarcity of food resources. This may suggests that seasonal changes in competition might be important in the evolution and maintenance of animal personalities in species whose population dynamics have a clear seasonal component.

Our results show that stress-sensitivity, quantified using a hole-board test, correlated with trappability, a common field measurement for boldness and risk taking in their natural environment. Indeed, trappability has been used either as a measurement for boldness (Le Cœur et al. 2015; Santicchia et al. 2018) or has been found to covary with boldness and exploration into a behavioural syndrome in several species (Garamszegi et al. 2009; Boyer et al. 2010; Wilson et al. 2011; Carter et al. 2012; Montiglio et al. 2012). However, this association between personality and trappability is absent in several small mammal species (Brehm and Mortelliti 2018; Jolly et al. 2019; Santicchia et al. 2020), as well as in *M. natalensis* (Vanden Broecke et al. 2018). Indeed, Vanden Broecke et al. (2018) found no link between trappability and exploration, but they did not measure stress-sensitivity due the use of a different experimental setup and is thus in line with our results. Nonetheless, these contrasting results in several small mammal species may suggest that that the link between personality and trappability is either species and/or environmental specific due to, for example, variation in predation pressure (Dingemanse et al. 2007). An alternative explanation for these contrasting results might also result from the use of different trapping methods (Stuber et al. 2013; Michelangeli et al. 2016) or because object familiarity (with for example the trap) has not always been taken into account, which might have a large, but so far understudied, effect. Indeed, our models suggested that stress-sensitivity affected recapture probability only when the individual was trapped during the previous night and was thus familiar with the object, while it was completely absent when they were not trapped during the previous night. This may indicate that effect of personality on trappability is more complex than has previously been hypothesized (Biro 2013; Michelangeli et al. 2016; Vanden Broecke et al. 2018). It also suggests that we were able to capture individuals over the whole stress-sensitivity continuum, with an overrepresentation of individuals with a low stress-sensitive personality, since they were recaptured more frequently.

Our results indicate that individuals with a low stress-sensitive personality are thus potentially bolder and take more risks in the wild suggesting that they exhibit a faster lifestyle compared to high stress-sensitive individuals (Réale et al. 2010; Mathot and Frankenhuis 2018). Within the POLS theory it is then expected that these bolder individuals, with a fast lifestyle, should have a lower survival probability (Réale et al. 2010; Dammhahn et al. 2018). However, we have found the opposite effect since our results revealed a negative correlation between survival and stress-sensitivity suggesting that bolder individuals live longer. This effect, however, was only present during the population decrease phase. While this seems to contradict the predictions of Wright et al., (2019), who suggested that bolder individuals should perform better in populations with low levels of intra-specific competition, it is in accordance with a recent meta-analysis of Moiron et al. (2020) who found that bolder individuals live significantly longer in the wild but not in the lab. They suggest that this is due to differences in food availability and competition among individuals (Moiron et al. 2020). Indeed, during the population increase phase, food is abundantly available and accessible for all individuals, especially due to the generalist diet (Mulungu et al. 2011) and lack of territoriality in *M. natalensis* (Borremans et al. 2014). Differences in personality among individuals should therefore have little effect on the individuals' food availability and subsequentially on their survival. This changes during the population decrease phase, where food becomes more limited and intra-specific competition increases (Leirs et al. 1990; Sluydts et al. 2007; Myers 2018). The observed personality dependent survival pattern during this period may suggest that bolder individuals, with a lower stress-sensitive personality, are more resistant against these high levels of competition potentially because they can gather more food resources. Indeed, bolder individuals take more risks during foraging which may result in a higher food intake and subsequently increase their survival rate (Ward et al. 2004; Bergvall et al. 2011; Dammhahn and Almeling 2012; Mella et al. 2015). An alternative explanation might be that that bolder individuals enter the population decrease phase with a higher body weight compared to more stress-sensitive individuals which has a positive influence on their survival during the period of food scarcity (Millar and Hickling 1990; Leirs et al. 1990; Krebs 2013). Indeed, Vanden Broecke et al. (2019) found that stress-sensitivity was correlated with density, where low stress-sensitive individuals were born earlier in the breeding season. These individuals have therefore experienced a prolonged period where food was abundantly available compared to high stress-sensitive individuals and should therefore have a higher body weight at the end of the population increase phase.

However, the effect of personality on survival was only present in males and completely absent in females. A potential explanation for this result might lie in the predicted trade-off between survival and reproductive success within the POLS framework (Réale et al. 2010; Dammhahn et al. 2018; Hämäläinen et al. 2018; Mathot and Frankenhuis 2018) which may differ between males and females. Indeed, reproductive success varies strongly between the two sexes, where almost all adult females reproduce during their lifetime (Sluydts et al. 2009), while male reproductive success is highly skewed with a small percentage fathering all offspring in a population (Kennis et al. 2008). We therefore argue that the trade-off between survival and reproductive success is more pronounced in male *M. natalensis* which would lead to a stronger, positive, correlation between stress-sensitivity and reproductive success in males compared to females. However we found no evidence for this trade-off since stress-sensitivity did not affect the individuals maturation age, which we used as a proxy for reproductive investment. This could be either because stress-sensitivity has no effect on reproductive success or that maturation age is not a good proxy for reproductive success. The latter might be the most plausible explanation since all animals will reach sexual maturity during their lifetime, but it does not necessarily correlate with effective reproductive success (Leirs et al. 1993; Kennis et al. 2008). It would therefore be interesting to perform parental assignments using microsatellites of all young individuals inside the enclosures to get a clear picture of the variation in reproductive success among individuals in order to study the link between survival and reproductive success.

Contrary to our expectations, exploration had no effect on either survival, maturation or recapture probability. This is an important finding since it may suggest that exploration, measured in the hole-board test, does not affect risk taking in the wild nor survival in *M. natalensis,* potentially due to species specific differences which are currently unknown. Indeed, exploration has been found to affect trappability in Siberian (*Tamias sibiricus*; Boyer et al. 2010) and eastern chipmunks (*T. striatus*; Montiglio et al. 2010) but not in several other rodent species (Brehm and Mortelliti 2018; Jolly et al. 2019; Santicchia et al. 2020). Similarly for survival, while exploration has been found to affect survival in several species (e.g. : Dingemanse et al. 2004; Bergeron et al. 2013; Rödel et al. 2015; Santicchia et al. 2018), large differences exist across different studies and species (Moiron et al. 2020).

In conclusion, our results suggest that stress-sensitivity affects both trappability and survival in wild *M. natalensis*, but only during periods of increased intra-specific competition. These results may have important consequences on the population scale, as well. During the population decrease phase, selection will favour males with a lower stress-sensitive personality. This will eventually lead to a higher proportion of these less stress-sensitive individuals ,within the population, at the beginning of the next breeding season, which has been found in Vanden Broecke et al. (2019), where less stress-sensitive individuals were caught more frequently at low densities. We therefore believe that seasonal variation in intra-specific competition has a large effect on the evolution and maintenance of animal personalities in species who experience large fluctuations in population size on a very short timescale, due to seasonal variations in food availability.

Acknowledgements: We would like to that the staff at the Pest Management Center (Sokoine University of Agriculture) for their excellence assistance during the fieldwork, specifically Shabani Lutea, Goefrey Sabuni, Omary Kibwana, Baraka Edson, Maddy Wheatley, Aurelia Bongers and Steven Van den Panhuyzen. Special thanks to Bert Thys for his assistance during the whole process.

Funding: BVB. was funded by the Ph.D. fellowship from the Research Foundation Flanders (FWO) (grant ID: 11A0817N).

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: All experimental procedures were approves by the University of Antwerp Ethical Committee for Animal Experimentation (LA1100135) and adhered to the EEC Council Directive 2010/63/EU and followed the Animal Ethics guidelines of the Research Policy of Sokoine University of Agriculture

Data accessibility: The data will be archived online on the Center for Open Science (OSF), a public and digital repository, should the manuscript be accepted.

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Table 1: Models to determine the effects of two personality traits, exploration and stress-sensitivity, on survival, maturation and recapture probability of M. natalensis during one population cycle. We first modelled survival followed by maturation and lastly recapture probability. Models are sorted within each step in ascending order by their AICc values, where models with the lowest AICc value (bold) were retained in the next modelling steps.

Survival		Maturation	Recapture	id	Deviance	AICc	ΔAICc
Population Increase	Population decrease						
1) Survival							
Stepwise reduction: Population increase							
Sx	**Sx * (E + St)**	**Sx**	**T**	**35**	**5132.70**	**5204.55**	**0.00**
Sx + St	Sx * (E + St)	Sx	T	36	5130.99	5204.95	0.40
Sx + E	Sx * (E + St)	Sx	T	36	5132.41	5206.37	1.82
Sx + St + E	Sx * (E + St)	Sx	T	37	5130.87	5206.94	2.39
Sx * St + E	Sx * (E + St)	Sx	T	38	5130.50	5208.69	4.14
Sx * E + St	Sx * (E + St)	Sx	T	38	5130.83	5209.02	4.46
Sx* (E + St)	Sx * (E + St)	Sx	T	39	5130.48	5210.78	6.23
Stepwise reduction: Population decrease							
Sx	**Sx * St**	**Sx**	**T**	**33**	**5135.30**	**5202.95**	**0.00**
Sx	Sx * St + E	Sx	T	34	5134.10	5203.84	0.90
Sx	Sx * (E + St)	Sx	T	35	5132.70	5204.55	1.60
Sx	Sx	Sx	T	31	5141.09	5204.55	1.60
Sx	Sx + St	Sx	T	32	5140.27	5205.82	2.87
Sx	Sx + E + St	Sx	T	33	5140.06	5207.71	4.76
Sx	Sx * E + St	Sx	T	34	5138.94	5208.68	5.74
2) Maturation							
Sx	**Sx * St**	**Sx**	**T**	**33**	**5135.30**	**5202.95**	**0.00**
Sx	Sx * St	Sx + St	T	34	5134.28	5204.02	1.08
Sx	Sx * St	Sx + E	T	34	5135.23	5204.98	2.03
Sx	Sx * St	Sx + E + St	T	35	5134.18	5206.03	3.08
Sx	Sx * St	Sx * E + St	T	36	5133.47	5207.43	4.48
Sx	Sx * St	Sx * St + E	T	36	5133.79	5207.75	4.80
Sx	Sx * St	Sx * (E + St)	T	37	5133.13	5209.20	6.25
3) Recapture probability							
Sx	**Sx * St**	**Sx**	**T * St**	**35**	**5125.77**	**5197.62**	**0.00**
Sx	Sx * St	Sx	T * St + E	36	5125.69	5199.65	2.03
Sx	Sx * St	Sx	T + St	34	5131.12	5200.87	3.24
Sx	Sx * St	Sx	T * (E + St)	37	5125.65	5201.72	4.10
Sx	Sx * St	Sx	T + E + St	35	5130.94	5202.79	5.17
Sx	Sx * St	Sx	T * E + St	36	5130.92	5204.88	7.25
Sx	Sx * St	Sx	T	32	5140.27	5205.82	8.19

Abbreviations: E, exploration; St = stress sensitivity; Sx = Sex (male or female); T = trap awareness (aware or unaware); Id = number of identifiable parameters; AICc = sample size corrected version of Akaike information criterion and ΔAICc = difference in AICc between the model and the model with the lowest AICc value within each modelling step.

Figure legends

Figure 1: The minimal number of animals alive in each enclosure (A = red, B = green, and C = blue), calculated for every trap session using the individuals' capture histories. The sample period is divided into two phases: the population increase phase (June – October) and the population decrease phase (November – April).

Figure 2: Survival probability for females (light blue) and males (dark red) in function of stress-sensitivity, a personality trait in *M. natalensis*, during both the (A) population increase and (B) decrease phase. Stress-sensitivity had no effect on survival during the population increase phase, but affected male survival during the decrease phase. Solid lines and ribbons represent the probability that an animal survived until next 14 days with their respective 95% confidence interval.

Figure 3: Recapture probability for trap aware (trapped during the previous trapping session; dark red) and unaware (not trapped during the previous trapping session; light blue) with their 95% confidence interval. Individuals with a higher stress-sensitive personality have a lower recapture probability than individuals with a lower stress-sensitive personality.

Figure 1

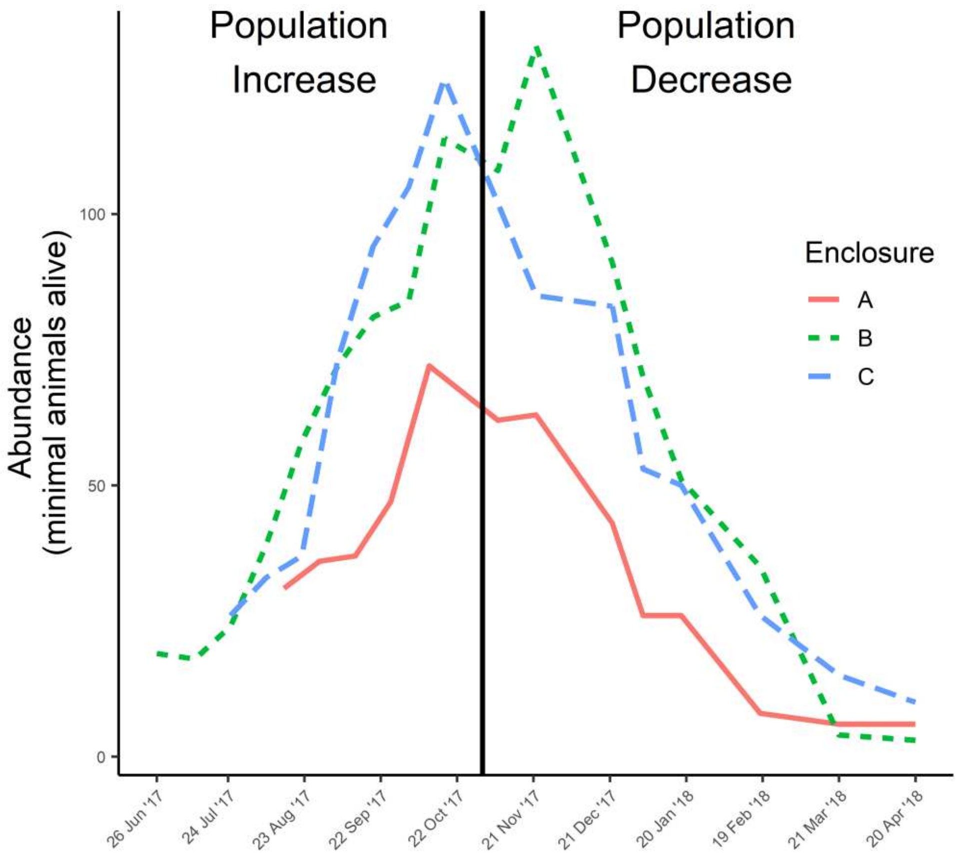

Population Increase
Population Decrease
Abundance (minimal animals alive)
100
50
0
Enclosure
A
B
C
26 Jun '17
24 Jul '17
23 Aug '17
22 Sep '17
22 Oct '17
21 Nov '17
21 Dec '17
20 Jan '18
19 Feb '18
21 Mar '18
20 Apr '18

Figure 2

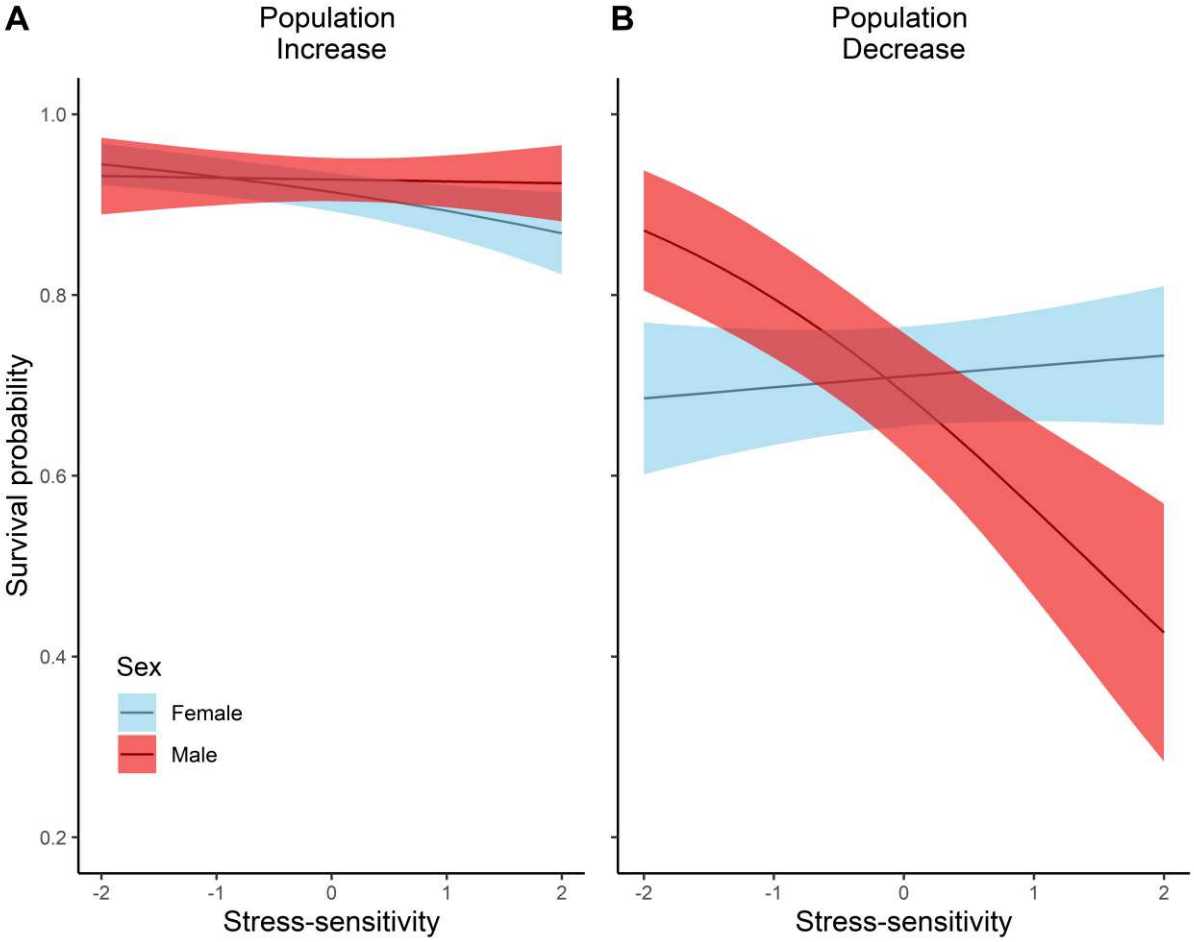
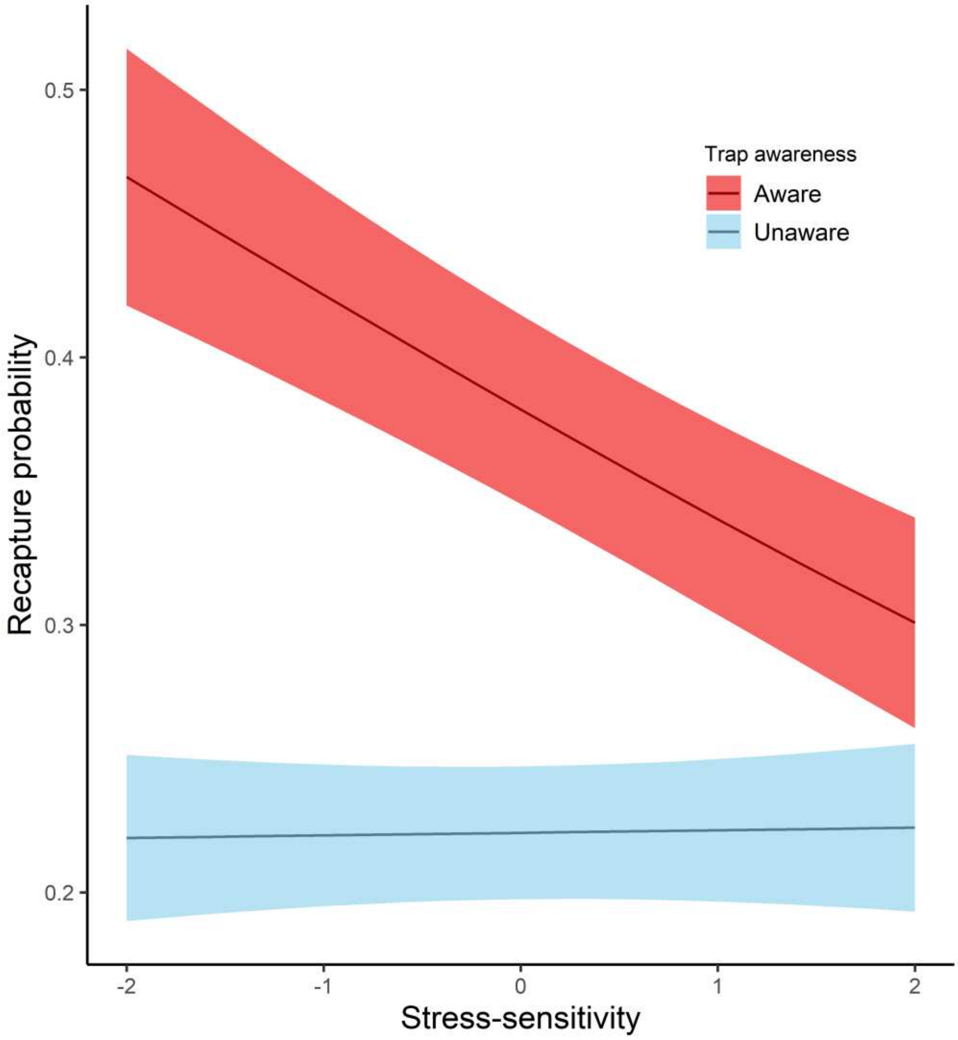

A
Population Increase
B
Population Decrease
Survival probability
1.0
0.8
0.6
0.4
0.2
Sex
Female
Male
-2
-1
0
1
2
Stress-sensitivity

Figure 3


Trap awareness
Aware
Unaware
Recapture probability
0.5
0.4
0.3
0.2
-2
-1
0
1
2
Stress-sensitivity