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The Amsterdam University College (AUC) Undergraduate Journal of Liberal Arts and Sciences is a biannual, interdisciplinary publication showcasing outstanding undergraduate academic papers. The Journal aims to demonstrate the strength of undergraduate scholarship at AUC, to reflect the intellectual diversity of its academic programme, to encourage best research and writing practices, to facilitate collaboration between students and faculty across the curriculum, and to provide students with opportunities to gain experience in academic reviewing, editing and publishing. The Editorial of the Journal is constituted of members of the InPrint board, a registered AUCSA committee.

Foreword

Welcome to the 14^{th} Capstone Issue!

Before graduation, all AUC students are required to write a Capstone thesis - an independent research paper in the disciplines of Science, Social Science or Humanities. The four-month writing process during the semester encourages students to engage with and contribute to the academic dialogue in their chosen field. In this Capstone Issue we publish six student Capstones, two from each major, written by AUC's graduating students of 2020.

The Capstones published in this issue have undergone rigorous selection and editing processes carried out by our Editorial Board. The aim of the editors is to improve the clarity and accessibility of the selected works, making them interesting to a general reader but maintaining a high standard in their academic field.

I would like to extend a word of thanks to the editors who worked tirelessly on the papers, meticulously caring for every minor detail – without them this publication would not have been possible. Thanks also goes out to the authors for their continued engagement in the process and for their patience with the long conversations regarding word choice and punctuation.

The papers in this edition cover topics ranging from Mexican cinema and the gender roles to earthworm behavioural differences, showcasing the variety of interests encouraged by a liberal arts and sciences education. I hope that this Capstone Issue can share a small slice of AUC students' academic work and interests – with our peers, our families, and more. Enjoy reading the issue!

Sarah Martinson, on behalf of InPrint

Sciences

The early bird catches the bold worm

Individual behavioural differences in the common earthworm (*Lumbricus terrestris*)

Rayne Leroux

Supervisor
Dr. Wouter Halfwerk (VU)
Reader
Dr. Cor Zonneveld (AUC)

Photographer: Jasmin Ronach

Abstract

In recent years, behavioural ecologists have become increasingly focused on animal personalities; individual differences in behaviour that are consistent across time and contexts. The majority of these studies focus on vertebrate species and little attention has been given to invertebrates. In this study, individual behaviour differences will be evaluated in the common earthworm (*Lumbricus terrestris*) by observing their activity levels and boldness as well as evaluating whether body weight is a factor related to these traits. The results indicate interindividual differences in activity and boldness, however, no significant relationship was found between the body weight of the earthworms, their activity levels, or boldness.

Keywords and phrases: *personality, individual variation, boldness, activity, earthworms*

Contents

1 Introduction

Animal personalities have become of increasing interest in behavioural ecology (Sih et al. 2004; Réale et al. 2007; Sih and Bell 2008; Réale et al. 2010); however, research on individual variation in invertebrate species remains limited (Kralj-Fiser and Schuett 2014). In this study, individual variation in the common earthworm (*Lumbricus terrestris*) will be analysed by measuring earthworm responses to a predator risk context and observing their activity levels. Earthworms have a significant impact on soil profiles by modifying their biological, chemical, and physical properties (Edwards and Bohlen 1996), and are as such frequently used in ecological research (Singh et al. 2019). Finding individual variation in the behaviour of *L. terrestris* will be applicable for future experiments and understanding how personality impacts the ecology and evolution of the species.

2 Research Context

The study of animal personality, also known as temperament, can be traced back to the early 20th century; however, it is only in the last few decades that this phenomenon was incorporated into the field of ecology (Sih et al. 2004; Réale et al. 2007; Réale et al. 2010; Kralj-Fiser and Schuett 2014; Ahlgren et al. 2015). It is found that in many species individuals vary in their behaviour from each other and this variation influences how they interact with their environment. Studies on animal personality are mainly based on the measurement of traits, su-ch as sociality or exploration. For instance, a species may exhibit an explorative trait where some individuals are more inclined to explore new areas than others. As a new concept to behavioural ecology, the definition of personality has been extensively debated (Réale et al. 2010; Koski 2011). The current consensus describes animal personalities as individual behavioural differences that are consistent over time and across contexts (Dall et al. 2004; Réale et al. 2007; Réale et al. 2010; Kralj-Fiser and Schuett 2014). In this definition, consistency implies that the differences between individuals will remain similar, but the trait values can change in individuals over time or across situations (Dall et al. 2004). Furthermore, personality does not only involve differences at an individual level, but can also describe differences between families or populations (Hayes and Jenkins 1997; Sih et al. 2004; Réale et al. 2007). The maintenance of a behavioural trait across different environments is called a behavioural carryover (Sih et al. 2004). For instance, an individual that is highly active in an environment with no predators will also show high activity in an area with predators. Behavioral carryover is also used to describe the consistency of a trait over different developmental stages, which is comparable to a trait that is displayed by an individual in two different environments (Réale and Dingmans 2010).

Individual variation in behaviour has often been assumed to correspond to an absence of behavioural plasticity, where plasticity refers to a change in behaviour in response to exposure to stimuli, such as a change in environmental conditions (Sih et al. 2004; Dingemanse et al. 2010; Koski 2011). However, research demonstrates a link between personality and individual plasticity (Koolhaas et al. 1999; Sih and Bell 2008), where highly consistent individuals express a limited part of the phenotypic variation of the population, and less consistent individuals exhibit most of the variation within the population. Therefore, variation in an individual's consistency corresponds to individual variation in plasticity (Bergmuller 2010; Réale and Dingemanse 2010). It should be noted that a highly consistent individual can also exhibit phenotypic plasticity, as the individual's behaviour can still change to adjust to its environment (Réale and Dingemanse 2010). Several theories have been proposed to explain why repetitive behaviour exists. The costs involved in maintaining flexibility are large in terms of energetics and acquiring information about the environment (DeWitt et al. 1998; Dall et al. 2004). Furthermore, environments are rarely predictable, which can lead to an unreliable assessment of cues and can give rise to individuals expressing phenotypes that poorly match their environment (DeWitt et al. 1998).

Réale et al. (2007) proposed five categories for animal traits to measure personality: (1) boldness, which encompasses an individual's reaction to a situation involving risk, such as encountering a predator; (2) exploration, which involves how an individual reacts to a new situation such as a novel object; (3) activity, which concerns the activity level of the individual and can influence the measurements of the two previous categories; (4) aggressiveness, which is where the agnostic response of an individual to their conspecifics is analysed; (5) sociability, which is where individuals may seek or avoid the presence of conspecifics. A phenotypic correlation between two behavioural traits is termed a behavioural syndrome (Gosling 2001; Sih et al. 2004; Krams et al. 2014). Syndromes that occur due to a common mechanism are important to identify because selection on one trait may shape behaviour in other contexts (Sih et al. 2004).

In several species, the aggressive-bold syndrome has been documented whereby bold individuals are more inclined to be aggressive to their conspecifics (Huntingford 1976; Bell 2005; Reaney and Backwell 2007). Boldness has also been associated with exploration and activity where bolder individuals tend to be explorative in novel situations and more active than shy conspecifics (Huntingford 1976; Koolhaas et al. 1999; Bell 2005). The correlation between boldness, activity, and aggression has been formalized as the reactive-proactive axis: a behavi-oural syndrome of the coping strategies of individuals to stressful situations. In this syndrome, proactive individuals are more bold, aggressive, active, explorative, and insensitive to environmental chan-ges in comparison to reactive individuals (Sih et al. 2004; Dal et al. 2004; Dingemanse et al. 2010). The aforementioned correlations coincide with research that has found several evolutionary and ecological consequences of the bold-shy continuum in different species. Studies have shown bold individuals to have more mating opportunities (Reaney and Backwell 2007), higher dispersal ranges (Dingemanse et al. 2003) and higher foraging rates (Ioannou et al. 2008), but also a higher mortality rate due to predation, in comparison to their shy conspecifics (Biro et al. 2004). There has been little research on the compromise of risk from predators for beneficial foraging, dispersal, and reproduction in bold individuals. A study by Ahlgren and others (2015) found that bold individuals can compensate for this by expressing phenotypic traits that reduce the risk of predation. Their results found a strong correlation between the shell shape of the aquatic wandering snail (*Radix balthica*) and their tendency towards risk-taking.

The study of personality differences has been valuable to society in a variety of ways, from improving animal welfare to predicting disease risk in humans (Réale et al. 2007). Furthermore, studying the personality of non-human animals can provide us with a better understanding of the effects of genetics, development, and the environment on human personality and its evolutionary origins (Gosling 2001; Bergmuller 2010). Individual variation in behaviour is commonly distributed in a non-random manner across specific axes (Gosling 2001), suggesting its likeness to have significant consequences to the ecology and evolution of species (Dall et al. 2004; Réale et al. 2007; Killen et al. 2017). One of these consequences is the tendency of a species to be invasive; dispersal plays an important role in the invasiveness of a species and it has been associated with boldness (Dingemanse et al. 2003), aggression, and high activity levels (Rehage and Sih 2004). Therefore, measuring the behavioural traits of an invasive species could be helpful in understanding their dispersion patterns and potential to invade new areas. Personality can also influence how well an individual may respond to a change in the environment. For example, reactive individuals respond better to environmental changes than proactive individuals as they are more sensitive to changes in their environment and approach novel situations with more caution (Sih et al. 2004; Dingemanse et al. 2009). Furthermore, personality can affect the distribution of individuals. For example, individuals with high activity and limited plasticity may be restricted to environments with low predation risk, whilst low activity types could make use of high predation risk areas (Sih et al. 2004). With regards to research on animal behaviour, accounting for personality when conducting research can avoid the issue of generating sampling bias (Biro and Dingemanse 2009). For instance, a study using only individuals that exhibit a particular trait, such as high aggression, would lead to bias results.

There has been a significant increase in the number of publications on animal personalities over the last few decades (Réale et al. 2010), however, the majority of personality studies have been conducted on vertebrates whilst invertebrate species have received little attention (Kralj-Fiser and Schuett 2014). Over 98% of all animal species are invertebrates and they have a wide range of characteristics and behaviours that are rare in vertebrate species, such as asexual reproduction and parasitism (Mather and Logue 2013; Kralj-Fiser and Schuett 2014). Investigating invertebrate personalities is essential to bro-adening our understanding of patterns of individual behavioural differences

(Mather and Logue 2013) and could provide explanations to the ultimate and proximate underpinnings of individual variation in personality where vertebrate studies have not been able to deliver (Kralj-Fiser and Schuett 2014). A literature search by Mather and Logue (2013) found only 32 papers that observed individual differences in invertebrates, including species within the phyla Arthropoda, Nematoda, and Mollusca. Currently, there are no studies on the personality of a species within the phylum Annelida.

Lumbricus terrestris, the common earthworm, is an anecic organism that builds deep vertical burrows in the soil and moves to the soil's surface to feed (Edwards and Bohlen 1996). It has been theorized that the function of their negatively phototactic behaviour is to guide them away from areas that experience strong light to avoid encounters with predators as well as desiccation risks (Sandhu et al. 2018). Earthworms are predated by a wide range of animals including the red fox (*Vulpes vulpes*), the European badger (*Meles meles*), and herring gulls (*Larus argentatus Pontoppidan*) (Catania 2008). Th-ese predators use their vision and olfaction to capture earthworms. Therefore, negative phototaxis may reduce the risk of predation from diurnal spec-ies, such as birds (Sandhu et al. 2018). Another predator of the common earthworm is the mole (*Tal-pidae*) that digs underground to forage and create vibrations that the earthworms detect and respond to, allowing them to escape to the soil's surface (Catania 2008).

Another antipredator behaviour exhibited by *L. terrestris* is the defence mechanism tonic immobility (TI), which is a state of reversible paralysis where the organism appears to be dead and is unresponsive to its surroundings (Ruxton et al. 2004). The behaviour is also known as death-feigning or thanatosis; however, these terms are misleading as animals exhibiting TI often display a position different from dead animals (Honma et al. 2006). Furthermore, TI is a secondary anti-predatory strategy as it occurs after the prey has been detected and physical contact has taken place, whereas thanatosis attempts to avoid initial detection from a predator (Humphreys and Ruxton 2018). Several hypotheses have been proposed for the functionality of this defence strategy, of which three concern the behaviour of the common earthworm. By exhibiting paralysis, the predator may struggle to detect the prey after dropping it or the predator may lose interest (Miyatake et al. 2004); this is particularly successful for evading predators such as birds that are attracted to prey movement (Jones et al. 2007). A second potential function for TI is that a paralysed individual is less likely to be predated than nearby non-paralysed conspecifics. In other words, the attention of the predator is diverted to prey that is not exhibiting TI (Miyataka et al. 2009). Lastly, TI can make the individual appear dead; some predators have an aversion to dead prey, as the assumed death may be related to disease, leading them to avoid consuming the prey (Humphreys and Ruxton 2018).

The consistency of TI within individuals has been associated with metabolism and activity. A study by Krams et al. (2014) observed a population of mealworm beetle larvae (*Tenebrio molitor*) and found that individuals with a higher metabolic rate exhibited a shorter duration of immobility when encountering a predator. A study on two avian species (*Euplectes afer* and *Passer montanus*) reported a negative correlation between the duration of TI and activity levels, where individuals exhibiting shorter durations of TI were more active (Edelaar et al. 20-12). Similarly, a study on the flour beetle (*Tribolium confusum*) found a negative correlation between activity levels and the duration of TI (Nakayama et al. 2010). TI is a suitable behavioural trait for studying boldness (Edelaar et al. 2012), where individuals that do not enter a state of immobility or enter TI for a short duration are considered bold individuals, and individuals that exhibit TI and remain in the state for a longer duration are considered shy individuals.

Studies have shown a link between personality differences and energy metabolism of individuals whereby individuals with a fast-paced life, such as a high metabolism, show high risk-taking behaviour (Réale et al. 2010b; Krams et al. 2014). For example, a study on the adzuki bean beetle (*Callosobruchus chinensis*) reported the duration of TI observed was influenced by body size (Hozumi and Miyataka 2005). Additionally, studies have found bold individuals to express phenotypic traits that reduce predation risk (Ahlgren et al. 2015); in the case of the earthworm, this trait could potentially be its body weight.

In this study, individual behavioural differences will be tested for in *L. terrestris* by observing one of their antipredator responses and activity levels. The earthworms will be tested under two different contexts: inducing the earthworm's TI response to predation using a shake method and observing the activity level of the earthworm. By analysing the results of these experiments, this paper aims to answer the following questions: Does *L. terrestris* exhibit individual variation in TI, TI duration, and activity levels? If so, do the findings support the existence of a bold-activity syndrome, and is there a relationship between the body weight of *L. terrestris* and the behaviours studied?

3 Materials and Methods

Twenty-five *L. terrestris* were obtained from an online bait shop and housed individually in opaque plastic containers filled with compost. To avoid 'motivational states', where the differing hunger level of the earthworms may have a confounding effect on their behaviour, the earthworms were fed ad libitum in a standardized manner to avoid hunger affecting their risk-taking behaviour and activity levels (Koolhaas et al. 1999). The body weight of each earthworm was recorded once before conducting trials with a digital scale ($\pm$0.001g) to analyse the effect of body weight on the behavioural traits boldness and activity.

Trials were conducted in an open field arena with dimensions 24 x 19 x 8 cm filled with 4 cm of soil. To distinguish between activity and exploratory behaviour, this soil was used to imitate the natural environment of the earthworm, meaning that they would exhibit activity rather than exploratory behaviour (which is instead investigated by testing animals in novel settings) (Réale et al. 2007). To measure boldness, a shake stimulus was applied to mimic the attack of a predatory bird. Tonic immobility was induced by seizing the earthworm at its midbody with forceps, shaking the individual side-to-side five times, and dropping it into the arena from 10cm above the soil. In each trial, TI was provoked and the duration of this behaviour was timed using a stopwatch. To measure activity, the locomotor activity of the earthworms was observed individually for five minutes after the boldness test. Activity levels were rated on a scale of 1 to 4 which are defined as: 1 is the lowest activity level and describes that the individual's head and/or tail moved but the body remained in the same starting area; 2 denotes that the individual's body moved but remained partially in the same starting area; 3 describes that the individual moved to a different area of the container; 4 is the highest activity level where the individual moved across $\geq$ 50% of the arena. To measure the consistency of the earthworms' behaviour, four trials were performed on each individual. To avoid habituation occurring, trials were conducted every three days. Repeating the same measures multiple times can lead to individuals habituating to the shake stimuli and their behaviour could become more or less responsive, which may bias the results (Martin and Réale 2008).

Data was collected from all twenty-five earthworms for each trial totalling to 100 observations for each behavioural trait measured. Statistical tests were conducted in R (R Core Team 2017). The intraclass correlation coefficient was used to estimate the consistency of the worm's behaviour; it is the most commonly used statistic to estimate repeatability in animal behaviour (Hayes and Jenkins 1997) and is a good indicator of individual consistency within a population (Réale and Dingemanse 2010). Repeatability is expressed as $r = \frac{S_A^2}{S_A^2+S^2}$ where the variables S_A^2 and S^2 stand for the variance among individuals and the variance within individuals respectively. The estimate ranges between one to zero; with an estimate of one, it is possible to predict an individual's exact behavioural value in future trials, whereas an estimate of zero indicates that it is not possible to make a prediction.

The aims of the experiment were to determine individual variation in exhibiting TI, TI duration, and activity levels in *L. terrestris* and whether there is a relationship between the body weight of individuals and these behaviours. A secondary aim was to determine if a bold-activity syndrome exists in *L. terrestris*.

To test for consistent individual differences in the behaviour of *L. terrestris*, the repeatability estimate of the behavioural measurements was determined. The r package $rptR$ (Stoffel et al. 2017) was used to implement the intraclass correlation coefficient with generalized linear mixed-effects models fitted. To test for consistency of TI duration within individuals a Poisson generalized linear mixed-effects model was fitted. In the model, TI duration was used as the response, body weight as a fixed effect, and the earthworm ID and trial number as random effects. The model was fitted within the $rptR$ function and bootstrapped 100 iterations. A similar approach was conducted to test for the repeatability of exhibiting TI using a binomial generalized linear mixed-effects model. To test for the repeatability of activity in the earthworms, the ordinal scale was converted to binomial data, as ordinal data was not suitable for this analysis. The scale of 1 to 4 was reduced to two categories: low activity (originally activity levels 1 and 2) and high activity (originally activity levels 3 and 4).

To test for a relationship between the earthworm's body weight and TI duration, a Poisson generalized linear mixed-effects model was fitted using the r package $lme4$ (Bates et al. 2015). In the model, TI duration was the response, and the earthworm ID was nested in the trial number and included as a random effect. Body weight was included as a fixed effect and a second model was fitted without body weight as an effect. To test for the significance of body weight on TI duration, the models were compared using ANOVA. A similar approach was conducted to test for the significance of the body weight of the earthworms on exhibiting TI and their activity levels. Binomial generalized linear mixed-effects models were fitted with TI or activity level as the response and the same random and fixed effects previously used.

To determine the existence of a bold-activity syndrome in *L. terrestris*, a correlation between TI duration and activity levels is required. Binomial generalized linear mixed-effects models were fitted with activity levels as the response, the earthworm ID as a random effect with trial number nested, and TI duration as a fixed effect in one of the models. A point-biserial correlation was conducted to find the strength of the correlation between the two traits.

4 Results

Repeatability of individuals exhibiting TI showed 50.8% of total variation attributed to difference among individuals (r = 0.508, standard error = 0.141, confidence interval = [0.22, 0.73], p-value < 0.001). Repeatability for the duration individuals would remain immobile was also high with 52.3% variation among individuals (r = 0.523, standard error = 0.112, confidence interval = [0.228, 0.68], p-value < 0.001). The repeatability for activity level was lowest with 31.8% variation among individuals (r = 0.318, standard error = 0.136, confidence interval = [0.038, 0.529], p-value = 0.00197). The results of the ANO-VA tests (Table 1) indicate that body weight is not a good predictor of exhibiting TI, TI duration, or activity level (p-value 0.121, 0.1526, 0.6832 > significance level 0.05). However, TI duration is a predictor for activity levels (p-value 0.0314 < 0.05). A point-biserial correlation between these two variables indicates a weak correlation (r_{pb}=-0.20601, p-value = 0.0398) where individuals with high activity show shorter durations of TI.

5 Discussion

Personality traits have been reported in numerous species across a wide range of taxa. In this report, personality in *L. terrestris* has been demonstrated by analysing the repeatability of boldness and activity traits. A meta-analysis on the repeatability of behaviour used 759 estimates from 114 studies on vertebrate and invertebrate species to determine a repeatability range of 0.35 $\leq$ r $\leq$ 0.52 with an average of 0.37 (Bell et al. 2009). In comparison to the meta-analysis, the results indicate the presence of a shy-bold axis in *L. terrestris* (repeatability estimate for exhibiting TI: r = 0.508, repeatability estimate for the duration of TI: r = 0.523). These high values for the repeatability of TI could be explained by three factors. Firstly, the repeatability of behaviour in invertebrates has been repor-ted to be higher than vertebrates for some behav-iours, with the meta-analysis showing repeatability values for invertebrates to be closer to the end of the range specified above (Bell et al. 2009). Secondly, research has shown that consistency is higher in individuals when trials are conducted over short intervals in comparison to long intervals (Bell et al. 2009). This study was conducted within three weeks, which is considered short for studies of animal behaviour. Lastly, TI is only one of the antipredator behaviours of *L. terrestris* and consists of two outcomes – the animal will either enter a state of TI or it will move. An experiment examining a different antipredator behaviour such as their response to vibrations caused by foraging moles would have more possible outcomes which could lead to a repeatability estimate for boldness different from the one found by this study.

In this study, shy individuals are individuals that

Response	Fixed effect	ANOVA results						
		AIC	BIC	logLik	Dev.	χ^2	Df	p-value
TI response	-	124.59	132.41	-59.297	118.59			
	body weight	124.55	134.97	-58.274	116.55	2.046	1	0.1526
TI duration	-	543.84	551.65	-268.92	537.84			
	body weight	543.44	553.86	-267.72	535.44	2.3951	1	0.1217
Activity level	-	133.82	141.64	-63.911	127.82			
	body weight	135.66	146.08	-63.828	127.66	0.1668	1	0.683
Activity level	-	133.82	141.64	-63.911	127.82			
	TI duration	131.19	141.61	-61.596	123.19	4.6302	1	0.0314

Table 1 ANOVA results. (Dev. = Deviance)

exhibited TI most frequently and bold individuals are individuals that immediately moved after encountering the stimulus. Shy individuals are more likely to exhibit TI during a predation attack; this behaviour deters the predator to attack further, wh-ich increases the probability of the individual's survival (Miyatake et al. 2004). A review of TI in beetles and moth larvae reported individuals who entered an immobile state were discovered and consumed less frequently by predatory birds than active conspecifics (Steiniger 1936). In contrast, bold individuals that do not exhibit TI may benefit when encountering a slow-paced predator such as some carnivorous insects (Ritter et al. 2016). However, it is not possible to conclude how this behaviour affects the fitness of *L. terrestris* as there are a multitude of behaviours that affect the likelihood of a predator capturing and consuming an individual (Lind and Cresswell 2005). For example, in this study, earthworms remained immobile for 5 seconds on average; it is plausible that this amount of time is sufficient for individuals to survive an attack. However, the actual outcome of an attack depends on the type of predator and their attention span, which differs between species.

The repeatability estimate for activity levels in this study was relatively low (r = 0.318) compared to the meta-analysis (Bell et al. 2009), but is accounted for in the repeatability value range of 0.30 - 0.50 from a study by Réale and colleagues (2007). To avoid the issues arising in the analysis of ordinal data, a future experiment to measure the activity of worms could collect continuous data, such as measuring the overall distance or average speed of the earthworms using motion tracking equipment. In this study, active individuals expressed high activity levels with a fast pace and frequent movement, whereas less active individuals expressed low activity levels with a slow pace and minimal movement. These activity traits of earthworms relate to behaviours in their natural environment; active individuals may have a higher chance of encountering predators in the wild (Killen et al. 2017), however, it is also possible that active individuals dig more burrows which would enable them to escape fossorial predators, such as moles, quicker than less active individuals.

Although all three repeatability estimates are high, there is the possibility that some individuals were more consistent in their behaviour than others (Dall et al. 2004; Bell et al. 2009). Differences in the consistency of an individual's behaviour can affect the repeatability estimate; individuals that are less consistent will reduce the repeatability estimate whilst individuals that are highly consistent will increase the estimate (Réale and Dingemanse 2010). A future study could involve measuring the individual plasticity and the repeatability of boldness and activity of *L. terrestris* using a framework based on the theory of behavioural reaction norms proposed by Dingemanse and others (Dingemanse et al. 2010). This would involve examining the relationship between the anti-predatory response of individuals across an environmental gradient (i.e. different risks of predation).

Studies have established an association between morphological and behavioural traits in species, such as the size of shell relating to boldness in wandering snails (Ahlgren et al. 2015). In this study, no relationship was found between the body weight and boldness of *L. terrestris* or the body weight and activity levels of *L. terrestris*, which suggests body weight is not related to boldness or activity in earthworms. A plausible reason that no relationship was found is due to the small range in body weight of the twenty-five individuals sampled, where 84% of individuals fell within a 3g range (4g - 7g). All of the earthworms sampled were obtained in a single order from a bait shop. Assuming the earthworms are raised in the same environment, it would suggest environmental conditions have less influence on variation in TI and activity than other factors, such as genetics, because there would be no variation in environmental effects between the worms.

As previously mentioned, correlated relationships between behavioural traits such as boldness and aggression have been observed in a wide variety of species. A weak negative correlation (r_{pb} =-0.20601) was found between the activity levels and the TI duration of the earthworms, indicating that some individuals who exhibited high activity levels presented shorter durations of TI. The result corresponds qualitatively with the studies previously presented; however, it cannot be stated that a bold-activity syndrome exists in *L. terrestris* due to an experimental error. During the trials, the observations of activity levels were conducted directly after the stimulus test. Therefore, the behaviour induced by the stimulus may have continued into the observations of activity, meaning that the two observations may not have been entirely independent.

When the results of this study are placed in a broader context, the consequence of individual variation in the boldness and activity of *L. terrestris* on their ecology can be inferred. Earthworms are important ecosystem engineers; they influence their environment through burrowing, producing casti-ngs, and litter fragmentation, all of which affect functions of an ecosystem such as nutrient cycling, soil carbon sequestration, and water infiltration (Si-ngh et al. 2019). The presence of an activity trait in *L. terrestris* has the potential to affect the function rates of an ecosystem: an ecosystem with a substantial portion of low activity types may have lower rates of functions, such as infiltration, than an area with high activity types. This reduced functioning would affect the growth of plants in the soil as well as the distribution and abundance of other soil fauna, having large-scale effects on the entire system.

Earthworms use vibrational cues to detect predatory moles (Catania 2008); it can be assumed that bold individuals would be slower or less likely to attempt to flee to the surface during an encounter with a mole than those less bold. If bold individuals are less responsive to vibrations, then it is plausible they are more tolerant of certain vibration levels than shy individuals. A difference in responses to vibrations could create a species distribution of bolder individuals inhabiting areas with higher levels of vibrations such as locations near wind turbines. Additionally, environments with different predation pressure on earthworms may select for more bold individuals if predators are generally slow pa-ced. As previously stated, boldness and high activity have been associated with proactive coping strategies where individuals are less responsive to changes in the environment. Bold or high activity earthworms may not efficiently adapt to new conditions in comparison to reactive individuals. For example, earthworms are poikilothermic, meaning their activity and metabolism are affected by temperature (Edwards and Bohlen 1996). Therefore, if the temperature of their environment increases, highly active individuals may struggle to adapt their behaviour, increasing their probability of mortality due to starvation or physical exhaustion. The limited plasticity that is often associated with proactive individuals is important to consider in our current climate crisis as global temperatures are predicted to increase and droughts will become more frequent (Singh et al. 2019).

At present, no research has been published on the personality traits of species within the phylum Annelida. The present findings provide supporting evidence for the existence of individual differences in the behaviour of the common earthworm. Individual variation with regards to boldness and activity traits of *L. terrestris* has been identified in this study. No relationship was detected between the body weight and boldness, or the body weight and activity levels of *L. terrestris*. Furthermore, a bold-activity syndrome was not determined in *L. terre-stris*. Whilst these relationships were not detected in this study, it is conceivable that they exist but require different experimentation methods to be identified. The findings from this study are a useful addition to the growing body of research on animal personalities. More specifically, these results are an important step towards addressing the ecological and evolutionary consequences of personality in the common earthworm, a species that has a significant impact on the biological, chemical, and physical properties of the soil on a global scale. This study has given rise to many questions in need of further investigation. Future studies should investigate the interindividual variation of antipredator responses and activity levels in a range of contexts to test the plasticity of these traits in *L. terrestris* and examine the mechanisms behind them.

References

Ahlgren J, Chapman BB, Nilsson PA, Bronmark C. 2015. Individual boldness is linked to protective shell shape in aquatic snails. Biol. Lett. 11: 20150029. doi: 10.1098/rsbl.2015 .0029

Bates D, Machler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using {lm e4}. J. Stat. 67(1): 1-48. doi: 10.18637/jss .v067.i01

Bell AM. 2005. Differences between individuals and populations of three-spined stickleback. J. Evol. Biol. 18: 464–473. doi: 10.1111/j.142 0-9101.2004.00817.x

Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. Anim. Behav. 77:771-783.

Bergmuller R. 2010. Animal personality and behavioural syndromes. In: Kappeler, P, editor. *Animal Behaviour: Evolution and Mechanisms*. Springer-Verlag Berlin Heidelberg. p. 587 - 621.

Biro PA, Abrahams MV, Post JR, Parkinson EA. 2004 Predators select against high growth rates and risk taking behaviour in domestic trout populations. Proc. R. Soc. Lond. B 271: 2233–2237. doi:10.1098 /rspb.2004.2861

Biro PA, Dingemanse NJ. 2009. Sampling bias resulting from animal personality. Trends Ecol. Evol. 24:66-67. doi: 10.1016/j.tree.2008.11 .001

Catania KC. 2008. Worm Grunting, Fiddling, and Charming—Humans Unknowingly Mimic a Predator to Harvest Bait. PloS ONE. 3(10): e3472. doi: 10.1371 /journal.pone.0003472

Dall SRX, Houston AI, McNamara JM. 2004. The behavioral ecology of personality: consistent individual differences from an adaptive perspective. Ecol. Letters. 7:734-739. doi: 10.1111/j.1461-0248.2004 .00618.x

DeWitt TJ, Sih A, Wilson DS. 1998. Costs and limits of phenotypic plasticity. Trends Ecol. Evol. 13:77-81. doi: 10.1016/s0169-5347(97)012 74-3

Dingemanse NJ, Both C, Van Noordwijk AJ, Rutten AL, Drent PJ. 2003. Natal dispersal and personalities in great tits. Proc. R. Soc. Lond. Ser. B. 270: 741–747. doi: 10.1098/rspb. 2002.2300

Dingemanse NJ, Kazem A, Réale D, Wright J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends Ecol. Evol. 25(2): 81–89. doi: 10.1016/j.tree.2009 .07.013

Edelaar P, Serrano D, Carrete M, Blas J, Potti J, Tella JL. 2012. Tonic immobility is a measure of boldness toward predators: an application of Bayesian structural equation modelling. Behav. Ecol. 23:619–626. doi: 10.1093/beheco/ars006

Edwards CA, Bohlen PJ. 1996. Biology and ecology of earthworms, Volume 3. Springer Science & Business Media

Gosling SD. 2001. From mice to men: What can we learn about personality from animal research? Psychol. Bull. 127(1): 45-86. doi: 10.1037/0033-2909.127.1.45

Hayes JP, Jenkins SH. 1997. Individual variation in mammals. J. Mammal. 78(2): 374-293. doi: 10.2307/1382882

Honma A, Oku S, Nishida T. 2006. Adaptive significance of death feigning posture as a specialized inducible defence against gape-lim-ited predators. Proc. R. Soc. B. 273(1594): 1631–1636. doi: 10.1098/rspb.2006.3501

Hozumi N, Miyatake T. 2005. Body-size dependent difference in death-feigning behavior of adult Callosobruchus chinensis. J. Insect. Behav. 18:557–566. doi: 10.1007/s10905-005-5612-z

Humphreys R, Ruxton G. 2018 A review of thanatosis (death feigning) as an anti-predator behaviour. Behav. Ecol. Sociobiol. 72(2): 1–16. doi: 10.1007/s00265-017-2436-8

Huntingford FA. 1976. The relationship between anti-predator behaviour and aggression am-ong conspecifics in the three-spined stickleback. Anim. Behav. 24: 245–260. doi: 10.1016/S0003-3472(76)80034-6

Ioannou CC, Payne M, Krause J. 2008 Ecological consequences of the bold–shy continuum: the effect of predator boldness on prey risk. Oecologia. 157: 177–182. doi: 10.1007/s0044 2-008-1058-2

Jones MP, Pierce KE, Ward D. 2007. Avian vision: a review of form and function with special consideration to birds of prey. J. Exot. Pet. Med. 16:69–87. doi: 10.1053/j.jepm.2007.03.012

Killen SS, Calsbeek R, Williams TD. 2017. The Ecology of Exercise: Mechanisms Underlying Individual Variation in Behavior, Activity, and Performance: An Introduction to Symposium. Integr. Comp. Biol. 57(2): 185-194. doi: 10.1093/icb/icx083

Kralj-Fiser S, Schuett W. 2014. Studying personality variation in invertebrates: why bother? Anim. Behav. 91:41-52. doi: 10.1016/j.anbehav.2014.02.016

Krams I, Kivleniece I, Kuusik A, Krama T, Freeberg T, Mänd R, Ljubova S, Rantala MJ, Mänd M. 2014. High Repeatability of Anti-Predator Responses and Resting Metabolic Rate in a Beetle. J. Insect Behav. 27(1): 57–66. doi: 10.1007/s10905-013-9408-2

Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, Van Reenen CG, Hopster H, De Jong IC, Ruis MAW, Blokhuis HJ. 1999. Coping styles in animals: current status in behavior and stress-physiology. Neurosci. Biobehav. Rev. 23: 925-935. doi: 10.1016/S0149-7634(99) 00026-3

Koski SE. 2011. How to Measure Animal Personality and Why Does It Matter? Integrating the Psychological and Biological Approaches to Animal Personality. In: Inoue-Murayama, M, Kawamura, S, Weiss, A, editors. *From Genes to Animal Behavior Social Structures, Personalities, Communication by Color*. Spr-inger. p. 115-137.

Lind J, Cresswell W. 2005. Determining the fitness consequences of antipredator behaviour. Behav. Ecol. 16(5): 945-956. doi: 10.1093/beheco/ari075

Martin JGA and Réale D. 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks. *Tamias striatus*. Anim. Behav. 75: 309–318. doi: 10.1016/j.anbehav.2007.05.026

Mather JA, Logue DM. 2013.The bold and the spineless: invertebrate personalities. In: Carere, C, Maestripieri, D, editors. *Animal personalities: Behavior, physiology, and evolution*. Chicago, IL: University of Chicago Press. p. 13-35.

Miyatake T, Katayama K, Takeda Y, Nakashima A, Sugita A, Mizumoto M. 2004. Is death-feign-ing adaptive? Heritable variation in fitness difference of death-feigning behaviour. Proc. R. Soc. B. 271:2293–2296. doi: 10.1098/rspb.2004.2858

Miyatake T, Nakayama S, Nishi Y, Nakajima S. 2009. Tonically immobilized selfish prey can survive by sacrificing others. Proc. R. Soc. B. Biol. Sci. 276:2763–2767. doi: 10.1098/rspb.2009.0558

Nakayama A, Yusuke N, Takahisa M. 2010. Genetic Correlation Between Behavioural Traits in Relation to Death-Feigning Behaviour. *Population Ecol*. 52(2): 329–335. doi: 10.1007/s10144-009-0188-7

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.o rg

Réale D, Dingemanse NJ. 2010. Personality and individual social specialisation. In: Szekely, T, Moore, AJ, Komdeur, J, editors. *Social Behaviour: Genes, Ecology and Evolution*. Cambridge University Press. p 417 - 441

Réale D, Dingemanse NJ, Kazem AJN, Wright J. 2010. Evolutionary and ecological approaches to the study of personality. Phil. Trans. R. Soc. B. 365: 3937 - 3946. doi: 10.1098/rstb.201 0.0222

Réale D, Garant D, Humphries MM, Bergeron P, Car-eau V, Montiglio PO. 2010b. Personality and the emergence of the pace-of-life syndrome concept at the population level. Phil. Trans. R. Soc. B. 365(1580): 4051-4063. doi: 10. 1098/rstb.2010.0208

Réale D, Simon M. Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. Biol. Rev. 82:291-318. doi: 10.1111 /j.1469-185X.2007.00010.x

Reaney LT, Backwell PRY. 2007. Risk-taking behavior predicts aggression and mating success in a fiddler crab. Behav. Ecol. 18: 521–525. doi: 10.1093/beheco/arm014

Rehage JS, Sih A. 2004. Dispersal behavior, boldness, and the link to invasiveness: a comparison of four Gambusia species. Biol. Invasions. 6: 379-391. doi: 10.1023/B:BINV. 0000034618.93140.a5

Ritter C, De Mol F, Richter E, Struck C, Katroschan KU. 2016. Antipredator Behavioral Traits of some Agriotes Wireworms (Coleoptera: Elateridae) and their Potential Implications for Species Identification. J. Insect Behav. 29:214–232. doi: 10.1007/s10905-016-955 5-3

Ruxton GD, Sherratt TN, Speed MP. 2004. Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry, Oxford Univ Press. doi: 10.1093/acprof:oso/978019852 8609.001.0001

Sandhu P, Shura O, Murray RL, Guy C. 2018. Worms make risky choices too: the effect of starvation on foraging in the common earthworm (*Lumbricus terrestris*). Can. J. Zool. 96: 1278-1283. doi: 10.1139/cjz-2018-0006

Sih A, Bell AM. 2008. Insights for Behavioral Ecology from Behavioral Syndromes. Adv. Study Behav. 38 227–281. doi: 10.1016/S0065-3454(08)00005-3

Sih A, Bell AM, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary ove-rview. Trends Ecol. Evol. 19(7): 372-378. doi: 10.1016/j.tree.2004.04.009

Singh J, Schädler M, Demetrio W, Brown GG, Eisenhauer N. 2019. Climate change effects on earthworms - a review. *Soil Org*. 91(3):114 – 138. doi:10.25674/so91iss3pp114

Steiniger F. 1936. Die Biologie der sog. „tierischen Hypnose“. In: Frisch, K, Goldschmidt, R, Ruhland, W, Vogt, W, editors. *Ergebnisse der Biologie*. Springer, Berlin, Heidelberg. p. 348-451

Stoffel MA, Nakagawa S, Schielzeth H. 2017. rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol. Evol. 8(110): 1639-1644. doi: 10.1111/2041-210X.12797

6 Appendix

Worm ID	Weight	Tria l	TI response	TI Duration (s)	Activity Level (ordinal)	Activity Level (binary)
1	4,39	1	1	2	3	1
1	4,39	2	1	5	4	1
1	4,39	3	1	4	4	1
1	4,39	4	1	3	4	1
2	5,02	1	1	5	2	0
2	5,02	2	0	0	1	0
2	5,02	3	0	0	2	0
2	5,02	4	1	7	3	1
3	5,53	1	1	13	4	1
3	5,53	2	1	6	3	1
3	5,53	3	1	10	4	1
3	5,53	4	1	8	4	1
4	5,47	1	1	21	2	0
4	5,47	2	1	11	4	1
4	5,47	3	1	5	3	1
4	5,47	4	1	5	3	1
5	6,33	1	1	16	2	0
5	6,33	2	1	24	2	0
5	6,33	3	1	8	3	1
5	6,33	4	1	5	3	1
6	6,31	1	1	4	2	0
6	6,31	2	1	13	2	0
6	6,31	3	1	13	2	0
6	6,31	4	1	9	2	0
7	5,16	1	0	0	2	0
7	5,16	2	0	0	2	0
7	5,16	3	0	0	3	1
7	5,16	4	0	0	2	0
8	4,07	1	1	17	3	1
8	4,07	2	1	12	2	0
8	4,07	3	1	5	2	0
8	4,07	4	1	8	2	0
9	4,08	1	0	0	2	0
9	4,08	2	0	0	3	1
9	4,08	3	0	0	2	0
9	4,08	4	0	0	3	1
10	9,41	1	1	15	2	0
10	9,41	2	1	10	1	0
10	9,41	3	1	8	3	1
10	9,41	4	1	15	3	1
11	7,86	1	0	0	4	1

11	7,86	2	0	0	4	1
11	7,86	3	1	9	4	1
11	7,86	4	1	6	4	1
12	6,09	1	0	0	3	1
12	6,09	2	0	0	4	1
12	6,09	3	1	10	4	1
12	6,09	4	1	5	3	1
13	7,76	1	1	9	2	0
13	7,76	2	1	9	2	0
13	7,76	3	1	17	2	0
13	7,76	4	1	7	2	0
14	5,93	1	0	0	3	1
14	5,93	2	1	8	3	1
14	5,93	3	0	0	4	1
14	5,93	4	0	0	4	1
15	7,03	1	0	0	2	0
15	7,03	2	1	13	2	0
15	7,03	3	0	0	3	1
15	7,03	4	1	10	2	0
16	6,20	1	0	0	3	1
16	6,20	2	0	0	4	1
16	6,20	3	0	0	4	1
16	6,20	4	0	0	4	1
17	4,68	1	0	0	3	1
17	4,68	2	0	0	2	0
17	4,68	3	1	5	1	0
17	4,68	4	0	0	2	0
18	4,56	1	1	7	1	0
18	4,56	2	1	20	3	1
18	4,56	3	0	0	3	1
18	4,56	4	1	6	3	1
19	4,65	1	1	5	2	0
19	4,65	2	1	7	3	1
19	4,65	3	1	8	2	0
19	4,65	4	0	0	3	1
20	4,02	1	1	14	2	1
20	4,02	2	0	0	3	1
20	4,02	3	0	0	4	1
20	4,02	4	0	0	4	1
21	6,01	1	0	0	3	1
21	6,01	2	0	0	2	0
21	6,01	3	0	0	3	1
21	6,01	4	0	0	3	1
22	4,25	1	0	0	1	0

22	4,25	2	0	0	2	0
22	4,25	3	0	0	3	1
22	4,25	4	0	0	2	0
23	6,67	1	1	9	2	0
23	6,67	2	1	15	2	0
23	6,67	3	0	0	3	1
23	6,67	4	0	0	3	1
24	4,90	1	1	14	1	0
24	4,90	2	1	13	3	1
24	4,90	3	1	5	3	1
24	4,90	4	0	0	3	1
25	4,50	1	1	16	3	1
25	4,50	2	0	0	3	1
25	4,50	3	0	0	2	0
25	4,50	4	1	8	3	1