acta ethologica (2019) 22:203–208
https://doi.org/10.1007/s10211-019-00327-5

ORIGINAL PAPER

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# Starvation decreases behavioral consistency in a Neotropical harvestman

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Received: 9 May 2019 / Revised: 12 September 2019 / Accepted: 26 September 2019 / Published online: 22 October 2019


**Abstract**

Consistent inter-individual differences in behavior have been shown in several animal groups, ranging from vertebrates to invertebrates. One of the most studied personality traits in animals is boldness, which is the tendency to expose to risky situations. Theory proposes that individuals' state (e.g., body energy) would influence the expression of personality traits. In this study, we tested if boldness levels of the harvestman *Mischonyx cuspidatus* (measured as duration of death feigning/freezing after simulated predator attack) differ between two different states, namely sated and food deprived. We also tested if the degree of repeatability in boldness is affected by the individual state. We found no differences in the levels of boldness expressed by *M. cuspidatus* when comparing between different conditions (sated and food deprived) at a population level. However, we found that individuals showed more consistency in boldness when sated relative to a food-deprived condition. Finally, we suggest new avenues for future studies addressing personality in harvestmen.

**Keywords** Arachnida · Boldness · Death feigning · Gonyleptidae · Opiliones · Personality

## Introduction

In non-human animals, the term personality has been used to describe intraspecific individual differences in behavior that are stable over time and across different contexts or situations (Carere and Maestripieri 2013). Several zoological groups show consistent individual differences in behavior (or repeatability), ranging from invertebrates to vertebrates (Bell et al. 2009; Kralj-Fišer and Schuett 2014). The traits that have been mostly studied in animal personality research so far are sociability, exploration tendency, activity, aggressiveness, and boldness (Gosling 2001; Koski 2014).

Boldness is a personality trait that refers to the way an individual reacts to a risky situation, with the bold being the individual that takes more risks and the shy the one that avoid taking risks (Réale et al. 2007; but See Watanabe et al. 2012 and Carter et al. 2013 for a discussion about the term "boldness"). It has been proposed that boldness is subject to a trade-off in which bolder individuals tend to have more access to resources, but, on the other hand, are prone to higher mortality and vice-versa (Sih et al. 2003, 2012). A meta-analysis investigating the fitness consequences of personality found some empirical evidence for the trade-off hypothesis (Smith and Blumstein 2008). Those results show that bold individuals tend to have higher reproductive success, but shorter life spans than shyer conspecifics (Smith and Blumstein 2008). At a population level, a high inter-individual variation in boldness would enable a species to inhabit different environments, because shy individuals would exhibit the highest survival in risky spots and bold ones would succeed more often in safe areas (Sih et al. 2012).

Recently proposed, the state-behavior feedback theory suggests that the state of individuals (i.e., body size and energy

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s10211-019-00327-5) contains supplementary material, which is available to authorized users.

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reserves) would influence the expression of their personality traits (Sih et al. 2015). This influence could result in different levels of behavioral expression, such as behaving more or less bold (Sih et al. 2015). Furthermore, the state of individuals can also influence the behavioral consistency of individuals (Pruitt et al. 2011; Lichtenstein et al. 2016; Wexler and Scharf 2017). One way of testing the influences of body energy on a personality trait would be testing animals in sated and a food-deprived condition, since it is well known that energy reserves are typically depleted by starvation (Castellini and Rea 1992; Arrese and Soulages 2010). Moreover, it is known that starvation influences several behaviors. For example, the attraction to food odors, probability of attacking prey, cannibalism, and fight between conspecifics showed a tendency to increase under starvation (reviewed in Scharf 2016). On the other hand, a trend of decrease was reported in sex-related behaviors such as releasing and response to pheromones, mating frequency, mating duration, and behaviors related to defense such as light avoidance and death feigning (Scharf 2016).

Death feigning (AKA playing dead, playing possum, tonic immobility, thanatosis, immobility reflex, contact defense immobility, and catatonia) (Edelaar et al. 2012) is a behavior in which animals stay inert after an encounter with a predator (Edmunds 1974; Ruxton et al. 2004). The effectiveness of death feigning has been shown in some empirical studies (Humphreys and Ruxton 2018 for a review). Due to their defensive function, passive defenses can be considered a proxy for level of boldness in animal personality studies. Thus, individuals that perform passive defenses more often and spend more time in those behaviors may be considered less bold than their conspecific counterparts that perform passive defenses less often and/or spend less time standing still (Tremmel and Müller 2012). Moreover, experimentally induced death feigning was found to be correlated with other anti-predatory behaviors, such as the activity in the presence of a model of a predator (Edelaar et al. 2012). Death feigning has been used as a proxy of boldness in arachnids such as spiders (Kralj-Fišer and Schneider 2012; Pruitt et al. 2012).

In this study, we used the Neotropical harvestman *Mischonyx cuspidatus* (Roewer 1913) (Arachnida: Opiliones: Gonyleptidae) as experimental model. The defensive strategies of this species encompass chemical defense, i.e., releasing a scent substance through a glandular opening located dorsoventrally in their body; retaliation i.e., pinching with pedipalps and sharp apophyses on their fourth pair of legs; freezing and death feigning (Segovia et al. 2015, 2019). We investigated whether the physiological state (sated and food deprived) of the harvestman *M. cuspidatus* influences its expression of boldness. More specifically, we tested whether (i) the levels of boldness differ between two body conditions (sated and food deprived) and (ii) whether body condition influences boldness consistency.

## Materials and methods

### Study species

We used *M. cuspidatus* in this study, because a previous work established an experimental protocol to induce death feigning and freezing in this species (Segovia et al. 2019). We collected females of *M. cuspidatus* on August 2017, at Parque Estadual do Tietê, São Paulo city, São Paulo State (23° 25′ S, 46° 28′ W). We housed the harvestmen individually in plastic boxes (13.5 cm; 9.5 cm; height 4.5 cm). Each plastic box had humid soil on the bottom and a bottle cap with a moistened ball of cotton inside to provide water and humidity. We fed the animals once a week alternating between banana or dog food (Pedigree Vital Pro ®), because this species is omnivorous as typical harvestmen (Acosta and Machado 2007). Dog food has been used in behavioral studies (Segovia et al. 2015, 2019), and harvestmen consume fruits in the wild (e.g., Machado and Pizo 2000). We maintained harvestmen under natural temperature (Mean = 22 °C° ± 3.6 "SD") and light cycle. Before starting the experiments, we fed all harvestmen for 4 weeks to standardize their body condition. We ran the experiments (see description below) between September and October of 2017.

### Boldness and effect of starvation

In this experiment, we tested whether (i) food deprivation affects the levels of boldness expressed in *M. cuspidatus* (i.e., the time that the individuals spend performing passive defenses, that is freezing and death feign); and (ii) food deprivation affects the boldness consistency in *M. cuspidatus*. To induce death feigning, we followed the protocol of Segovia et al. (2019). Briefly, we held the harvestmen by the femur of a leg IV and released the animals on their terrarium from a height of about 20 cm. All tests were run between 10 am and 7 pm. We used the time that females of *M. cuspidatus* took standing still after being released as a proxy of boldness. Animals that took more time to resume movement after being disturbed were considered less bold and vice-versa. We defined death feigning as the posture in which the individuals flex all their legs against their own body (Fig. 1). Freezing was defined as standing still in any different posture from what we considered to be death feigning (see Segovia et al. 2019). All tests were video recorded and posteriorly analyzed by the same observer.

For the tests with sated individuals, food was removed immediately before the trials. A new trial was conducted in the following day (1 day after the animals were last fed). The trials in a food-deprived condition were run after 14 days of starvation. In the following day, the animals were tested again (after 15 days of starvation). To avoid biases, we assessed boldness of approximately half of the females first in the sated

**Fig. 1** Female of the harvestman *Mischonyx cuspidatus* (Arachnida, Opiliones) performing death feigning

and then in the food-deprived condition. The remaining females were tested first in the food-deprived and then in the sated condition. In the last meal prior to the trials, we fed the animals with both banana and dog food (Pedigree Vital Pro ®). In the group tested first in a food-deprived condition, we fed the harvestman once (after the period of starvation) before the tests in the sated conditions. With this procedure, we kept the same time between tests in both groups (first tested sated and then food deprived and vice-versa). All females of *M. cuspidatus* ($N = 73$) were tested twice in the two different conditions (sated and food deprived), in a total of four trials. The time between tests was of at least 1 day.

### Statistical analyses

We used 73 individuals in each trial, resulting in a total of 292 trials. We analyzed all data pooled together (i.e., considering cases that individuals performed and did not perform death feigning). Death feigning and freezing were both considered as proxies of boldness (i.e., behavioral trait linked to risk avoidance, see "Introduction" section) because the animals stood still in both behaviors, possibly avoiding risks. Individuals that did not engage in death feigning or freezing were given the duration time of 0 s (approx. 12% of the cases), whereas individuals that performed death feigning/freezing were given a value between 1 and 1200 s, the latter being the maximum duration of a trial (approx. 2% of the cases).

In order to test if the number of individuals exhibiting passive defenses differed among the four trials, we ran chi-square tests. We used a generalized linear mixed model with a negative binomial error distribution to evaluate differences in the time of passive defenses (freezing/death feigning) (response variable) among fasting days (predictor). We added individual identification as a random variable in the model. We also rescaled the time of death feigning/freezing between 0 and 1 using rescale function of scales package.

We performed a general linear mixed model to test for the significance of the repeatability (behavioral consistency) of boldness ($r$) within and between fasting treatments using rptR package (Nakagawa and Schielzeth 2010). To evaluate repeatability within and between treatments, we estimated r for repeatability within sated (days 0 and 1) and food-deprived conditions (days 14 and 15), and across fasting treatments. Higher numbers of $r$ indicate higher behavioral consistency. In each analysis, we included the duration of death feigning/freezing (i.e., boldness) as the response variable, condition (sated vs food-deprived), the order of testing (sated first or food-deprived first) and the fasting days as fixed predictors, and individual identification as random variable. We only removed the condition for fixed predictor when we analyzed the repeatability within fasting treatments. We used the square root of the time duration of death feigning/freezing in the model with only starved individuals to attend test assumptions. The distribution of harvestman identification used in the models can be found in Fig. S1. We compared the $r$ values corresponding to fasting and starved treatments using a $t$ test. All data analyses were conducted in the R software, version 3.4.4 (R Development Core Team 2018).

## Results

There were no differences in the number of individuals performing passive defenses ($\chi^2 = 0.436$; d.f. = 3; $p = 0.933$) among the four trials (two not sated and two food deprived) (Table 1). The differences in the duration of the passive defenses did not differ between body conditions (Table 2). We found repeatability in *M. cuspidatus* within the sated condition ($r = 0.404$, SE = 0.096, 95% credible interval (hereafter CI) = 0.223–0.594, $p < 0.001$), but not in the food-deprived condition ($r = 0.185$; SE = 0.109, CI = 0–0.410, $p = 0.062$). Individuals in sated condition exhibited a 2.2 times greater consistency in death feigning/freezing duration than harvestmen in food-deprived condition ($t = 2.096$, d.f. = 190, $p = 0.037$). In general, the repeatability across fasting days was low ($r = 0.147$, SE = 0.057, CI = 0.040–0.261, $p = 0.003$).

**Table 1** Number of females of the harvestman *Mischonyx cuspidatus* (Arachnida, Opiliones) that performed passive defenses (death feigning and freezing) and time (in seconds) spent doing it (Median; Min; Max) in different body conditions

| Fasting days | Body condition | N° of individuals performing passive defenses ($N = 73$) |
|---|---|---|
| 0 | Sated | 61 (114; 3; 1091) |
| 1 | Sated | 60 (100; 1; 1186) |
| 14 | Food deprived | 61 (110; 3; 1.187) |
| 15 | Food deprived | 59 (98; 1; 1185) |

**Table 2** Results from a GLMM with negative binomial error distribution

| Fasting days | Body condition | *B* | SE | *z* | *P* |
|---|---|---|---|---|---|
| Intercept (Day 0) | Sated | − 1.999 | 0.305 | − 6.554 | < 0.001 |
| Day 1 | Sated | − 0.070 | 0.441 | − 0.159 | 0.874 |
| Day 14 | Food deprived | 0.179 | 0.423 | 0.424 | 0.672 |
| Day 15 | Food deprived | 0.189 | 0.416 | 0.456 | 0.648 |

The response variable is the time spent death feigning/ freezing (rescaled from 0 to 1) by females of the harvestman *Mischonyx cuspidatus* (Arachnida, Opiliones), the predictor variable is the number of days after being fed and individual identification is the random variable. The intercept corresponds to the reference level (day 0)

## Discussion

In this study, we have shown that the mean level of boldness expressed by females of the harvestman *M. cuspidatus* did not differ between sated and food-deprived conditions. However, *M. cuspidatus* showed higher behavioral consistency in a sated relative to a food-deprived condition. Therefore, boldness can be inconsistent when individuals are under food deprivation, but remain consistent in sated conditions.

Contrary to expectations, the body condition did not affect the number of individuals neither boldness consistency in *M. cuspidatus*. Our study contrasts with several studies showing the influence of environmental factors and individuals' state (sensu Sih et al. 2015) on duration and frequency of death feigning, such as body size (beetles: Hozumi and Miyatake 2005; snakes: Gerald 2008), age (decapods: Coutinho et al. 2013), sex (harvestmen: Segovia et al. 2019), previous copulation (beetles: Kuriwada et al. 2009), and period of the day (fowls: Rovee et al. 1976; beetles: Miyatake 2001a; spiders: Jones et al. 2011). With respect to feeding regime, previous studies have shown that beetles reared in a low-quality diet scored high in boldness (in this study, a cluster of behavior that included death feigning) (Tremmel and Müller 2012). Another study showed that the frequency of beetles performing death feigning was lower for food-deprived individuals when comparing to sated conspecifics (Miyatake 2001b). An important fact that could influence our results is that this species also relies on chemicals for defense (Hara et al. 2005). Thus, maybe some individuals are more prone to engage in passive defenses such as death feigning, but others would rely more on chemical defense independently of their state. Because we did not record the use of chemical defense in this study, this hypothesis needs further investigation.

Our results show boldness consistency in *M. cuspidatus* when individuals were sated. Several other studies have shown consistency in boldness-related behaviors in arachnids (Kralj-Fišer et al. 2012; Sweeney et al. 2013; Bosco et al. 2017; Chang et al. 2017). To give a few examples, the time that a fishing spider took to emerge to surface after being induced to diving was consistent within individuals when considering the different contexts of foraging and courtship (Johnson and Sih 2007). The time took by social spiders to resume movement after being stimulated with a puff of air (a stimulus designed to simulate a flying predator) was consistent within individuals (Keiser et al. 2014). The number of harassments required to induce black widow spiders to retreat was consistent within individuals (Halpin and Johnson 2014). However, to date, this is the first study to show behavioral consistency in harvestman.

We only found repeatability in boldness when individuals were tested sated compared to in a food-deprived condition. In beetles, it was found that a group fed under a low protein diet showed lower levels of behavioral consistency than the control group (Wexler and Scharf 2017). Similar results were found in black widow spiders that showed higher levels of consistency in their choosiness in habitat choice when sated than in a food-deprived condition (Pruitt et al. 2011). Accordingly, the spiders *Anelosimus aperta* and *Anelosimus studiosus* showed higher levels of repeatability in aggression and boldness than the food-deprived ones (Lichtenstein et al. 2016). Our findings point out in the same direction of previous studies with arthropods. Thus, we provide more empirical evidence for the role of body state on the stability of personality. One proposed explanation for the decreasing of repeatability in food-deprived animals is that some extreme personality types are costly. Thus, it would be only viable when food is plentiful (Pruitt et al. 2011; Lichtenstein et al. 2016), such that even higher ranked individuals would tend to show intermediate levels of behavior in situations of food deprivation. However, so far, the metabolic costs of passive defenses (death feigning/freezing) in harvestman are unknown. Therefore, the reasons why food-deprived *M. cuspidatus* show less consistency in behavior remain unclear. Additionally, unfavorable conditions could signal environmental unpredictability, elevating behavioral variability, and ultimately resulting in less behavioral consistency (Wexler and Scharf 2017).

Finally, we expect that our finding of behavioral consistency in *M. cuspidatus* contribute to new avenues of personality studies in harvestmen. These animals are potentially good models for several questions. To give some examples, it has been shown that females of *M. cuspidatus*, which lack weaponry, perform death feigning more often than males that bear sharp apophyses on their fourth pair of legs (Segovia et al. 2019). Since sexual dimorphism shares similarities with male-male dimorphism, it would be worthwhile testing for behavioral consistency in species with male dimorphism (see Buzatto et al. 2014). More specifically, one could look for consistent differences in behavior between major and minor males (minors are more similar to females) (Buzatto et al. 2014). If there is consistency in behavior of males, despite of their size, it is possible that these differences influence the outcomes of male-male interactions. It is also known that harvestmen have several lines of defense (Pomini et al. 2010). One could also investigate if there is any individual tendency in the use of particular defenses such as passive and chemical defenses. Another interesting question is whether death feigning is part of a behavioral syndrome with activity (Sih et al. 2012) in *M. cuspidatus*, testing the prediction that individuals that spend less time in death feigning are more active (see also Miyatake et al. 2008). In the end, we hope this work will encourage new personality studies in harvestmen.

**Acknowledgements** We thank Catalina Zuluaga, Cibele Biondo, Jerry Hogan, Laura Leal, Nathália Gonçalves, Patricia Izar, and Regina Macedo for providing suggestions on an early draft of this manuscript. Lucas Beltrami for outstanding assistance in laboratory tasks. We acknowledge the valuable suggestions of the editor Brigitte Weiß, Simona Kralj-Fišer and one anonymous reviewer.

**Funding information** Financial funding was provided by CAPES and Fundação de Amparo à Pesquisa do Estado de São Paulo (São Paulo Research Foundation, FAPESP): Proc. 2014/19191-3 to J.M.G.S, Proc. 2017/14196-5 to R.R.M. and 2015/01815-9 to R.H.W, which is also funded by CNPq 302879/2016-1.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest. The study complied with animal welfare regulation of our country/institutions.

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