



# Robustness in action: Leg loss does not affect mating success in male harvestmen

Ignacio Escalante<sup>1,2</sup> · Damian O. Elias<sup>1</sup>

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## Abstract

Defensive strategies, like other life-history traits favored by natural selection, may pose constraints on reproduction. A common anti-predator defense strategy that increases immediate survival is autotomy—the voluntary release of body parts. This type of morphological damage is considered to impose future costs for reproduction and fitness. We tested an alternative hypothesis that animals are robust (able to withstand and overcome perturbations) to this type of damage and do not experience any fitness costs in reproductive contexts. We explored the effects of experimental leg loss on the reproductive behavior of one species of Neotropical *Prionostemma* harvestmen. These arachnids undergo autotomy frequently, do not regenerate legs, and their courtship and mating necessitate the use of legs. We assessed the effect of losing different types of legs (locomotor or sensory) on courtship behavior and mating success in males. We found no differences in the mating success or in any measured aspect of reproductive behavior between eight-legged males and males that experienced loss of legs of any type. Additionally, we found that morphological traits related to body size did not predict mating success. Overall, our experimental findings support the null hypothesis that harvestmen are robust to the consequences of morphological damage and natural selection favors strategies that increase robustness.

## Significance statement

In order to survive encounters with predators, animals have evolved many defensive strategies. Some of those behaviors, however, can come with a cost to their overall body condition. For example, some animals can voluntarily lose body parts (tails, legs, etc.) to escape. This process can then affect many aspects of an animal's life, including reproduction. In a group of harvestmen (daddy long-legs) from Costa Rica, we tested the hypothesis that males are robust to the potential consequences of losing legs, and will not experience costs. We found that males that lost either legs used for locomotion or for sensory perception reproduced in the same way as animals with all of their legs. Consequently, we demonstrate that these arachnids are able to withstand the loss of legs with no effects on reproduction.

**Keywords** Autotomy · Daddy long-legs · Mating success · Opiliones · *Prionostemma* · Sexual behavior

## Introduction

Defensive strategies might compromise the body condition of animals, which can then affect their ability to reproduce. This dynamic can result in trade-offs between natural and sexual selection if strategies that ensure survival interfere with the ability to mate (Chenoweth et al. 2008; Sharma et al. 2012). On the one hand, defensive strategies that allow animals to escape predators and survive are favored by natural selection. On the other hand, behaviors and other traits that favor the likelihood of mating are favored by sexual selection. Previous work has explored trade-offs in morphological, physiological, and behavioral traits (Endler 1995;

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✉ Ignacio Escalante  
escalan3@uwm.edu

<sup>1</sup> Department of Environmental Sciences, Policy, & Management, University of CA—Berkeley, California, USA

<sup>2</sup> Present Address: Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, 3209 N Maryland Ave., Milwaukee, WI 53211, USA

Verhulst et al. 1999; Basolo and Alcaraz 2003). It has been found that visual ornaments and weapons (i.e., horns, antlers) may increase the risk of predation, even though those structures are crucial in competition for mates (Zuk and Kolluru 1998). For example, in environments with predators, male fishes had smaller sperm-transfer organs than in environments without predators (Langerhans et al. 2005). Similarly in male fireflies, higher signaling rates increased the likelihood of being predated (Woods et al. 2007), even though more conspicuous courtship signals are preferred by females (Branham and Greenfield 1996).

Certain defensive strategies that are favored by natural selection can compromise the overall body condition of an animal. To escape predators, many animal taxa have evolved the ability to voluntarily detach an appendage before or during a predator attack (Roth and Roth 1984; Fleming et al. 2007; Emberts et al. 2019). This defense strategy—known as autotomy—can increase immediate survival (Emberts et al. 2017, 2019). However, autotomy is often assumed to yield long-term consequences on fitness, as detached appendages or body parts often play a role in courtship, mating, or sperm transfer (reviewed in Emberts et al. 2019). Evidence regarding the effects of autotomy on reproduction is equivocal nonetheless, as the loss of body parts is known to bring negative, neutral, or even positive effects to reproduction (Emberts et al. 2019; Michaud et al. 2020; Cirino et al. 2021; García-Hernández and Machado 2021; Talavera et al. 2021). For example, after ‘tail’ autotomy, female scorpions experienced decreased fecundity, whereas males did not experience decreases in mating success (García-Hernández and Machado 2021). On the other hand, claw autotomy did not affect mating success in male crabs (McCambridge et al. 2016). Additionally, males and females of Coreidae insects invested more in testes growth after leg loss (Joseph et al. 2018; Somjee et al. 2018; Miller et al. 2019), and autotomized males produced more offspring than non-autotomized males (Cirino et al. 2021). The consequences of autotomy occur because autotomized individuals show altered courtship displays and/or diminished locomotor capabilities (Bateman and Fleming 2006; Emberts et al. 2019; García-Hernández and Machado 2021).

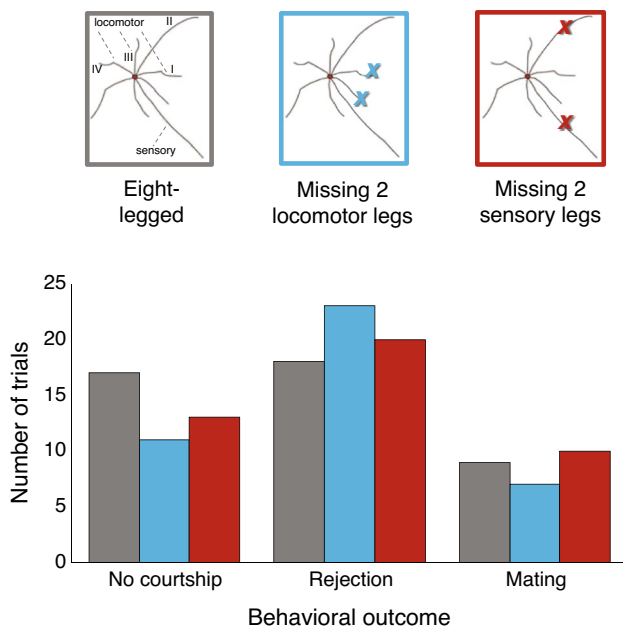
Alternatively, animals may have evolved robustness to variation in their own bodies so that autotomy does not affect reproduction. Robustness is the persistence of a behavior under environmentally induced perturbations (Kitano 2004). The robustness hypothesis then poses that animals have evolved mechanisms and traits to operate in the face of variable and challenging genetic and environmental conditions (Nijhout et al. 2017). For this study, we interpret robustness in autotomy as the ability of animals to contend (i.e., successfully mate) with variation in body form (i.e., leg loss and altered body plan caused by autotomy). Robustness and adaptability to bodily variation have been explored

in the fields of biomechanics (Mongeau et al. 2013; Clark and Tribblehorn 2014; Jayaram and Full 2016; Jayaram et al. 2018), systems biology (Kitano 2007; Félix and Wagner 2008; Lesne 2008; Nijhout et al. 2017), and even in the field of disability studies (Thomas 2007; Snyder and Mitchell 2010; Goodley 2016; Taylor 2017). Here, we expand on our previous work (Escalante et al. 2020, 2021; Escalante and Elias 2021), and formally test one robustness hypothesis in the context of behavioral ecology.

We study the effects of leg autotomy on mating success in *Prionostemma*, a Neotropical Sclerosomatidae harvestmen. This group of arachnids are ideal to explore this topic because autotomy is frequently high (Guffey 1999; Escalante et al. 2013, 2020, 2021; Domínguez et al. 2016; Powell et al. 2021a, b). Unlike most autotomizing animals, harvestmen do not regenerate legs before or after sexual maturity (Gnasparini and Hara 2007). In harvestmen, legs play a crucial role in reproduction for males (Willemart et al. 2006; Fowler-Finn et al. 2014, 2018, 2019; Machado et al. 2015). The North American *Leiobunum* males perform behaviors like leg wrapping and tangling during courtship and mating (Fowler-Finn et al. 2014; Sasson et al. 2020). These behaviors are crucial for mating (Fowler-Finn et al. 2014). In our study species, individuals use forelegs for extensive leg tapping behaviors during mating interactions. The sexual behavior of a congener of our study species has also been observed and similarly relies on leg behaviors during mating (Classen-Rodríguez, *unpubl.*). Altogether, these behavioral and morphological features suggest that there is strong selection on harvestmen to be robust and withstand the potential consequences of leg loss on reproduction.

Sclerosomatid harvestmen have two types of legs: locomotor and sensory (Fig. 1). Six legs (from pairs I, III, and IV) are locomotory and their primary function is movement (Sensenig and Shultz 2006; Escalante et al. 2019), but they are also used during mating interactions to position and sometimes restrain mates (Fowler-Finn et al. 2014). The second pair of legs are modified and specialized in sensory perception (Shultz and Pinto-da-Rocha 2007; Willemart et al. 2009). Sensory legs are used to probe the environment and to potentially detect and identify other individuals (Sensenig and Shultz 2006; Escalante et al. 2019). Interestingly, both locomotor and sensory legs are involved in courtship and mating (Fowler-Finn et al. 2014), and both leg types are frequently autotomized in *Prionostemma* harvestmen (Domínguez et al. 2016; Escalante et al. 2020; Escalante and Elias 2021).

We tested the null hypothesis that harvestmen are behaviorally robust to the potential consequences of leg loss on mating success and mating behavior against the alternative hypothesis of reproductive costs of autotomy. We experimentally induced autotomy of locomotor or sensory legs on eight-legged males. This procedure allowed us to control for types



**Fig. 1** Behavioral outcomes of the trials testing for the effect of the experimental loss of two different types of legs of males on the reproductive behavior of the Neotropical *Prionostemma* sp.5 harvestmen. The number of trials that ended in each type of outcome did not differ between treatments (see 9 for further statistical details). The top left diagram represents a harvestmen in top view (its proximal side is to the right) and the four leg pairs and types (locomotor or sensory) are labeled

of legs missing and the time since autotomy. We ran mating trials with eight-legged females and males with experimentally induced autotomy (as well as eight-legged males) and recorded the outcome of the trials (no courtship, rejection, or mating, see definitions below). This allowed testing a first prediction of the robustness hypothesis: that experimental leg loss of any type will not affect male mating success. We also quantified the duration of pre-copulatory interactions and mating behaviors in the trials. A second prediction of the robustness hypothesis we tested was that eight-legged and autotomized males will spend similar amounts of time performing pre-copulatory and mating behaviors. A third prediction we tested was that autotomized males would perform the same leg behaviors in courtship and mating with the remaining legs. With this framework, we explored whether behavioral plasticity may be the mechanism for robustness, allowing harvestmen to avoid any negative consequences of autotomy.

## Methods

### Study site and species

We conducted fieldwork at Las Cruces Biological Station, province of Puntarenas, Costa Rica (8° 47' N, 82° 57' W,

1200 m in elevation) from June 20 to August 08, 2017. We studied one undescribed species of *Prionostemma* (Sclerosomatidae: Opiliones) from Costa Rica for which previous research has examined their ecology and behavior (Grether and Donaldson 2007; Wade et al. 2011; Proud et al. 2012; Grether et al. 2014; Domínguez et al. 2016; Escalante and Elias 2021). To be consistent with that previous research (Proud et al. 2012; Escalante et al. 2019, 2020), we refer to our study species as 'sp.5.' Voucher specimens were deposited in the Essig Museum of Entomology at UC Berkeley.

### Field surveys, collection and animal care

To observe mating interactions in the field and note if interacting males and females had eight legs or if they were missing legs, we conducted nighttime field surveys. We searched for harvestmen in the forest floor from 20:00 to 0:00 h for 25 nights, as tropical harvestmen are active at nighttime (Proud et al. 2012). We sorted individuals as males or females based on their behavior and by using external morphological proxies (body size and shape). To verify that the external morphology proxies correspond with internal genitalia (the presence of fully developed ovipositor or penis), we dissected ten individuals of each putative sex. In the surveys, we collected adult eight-legged animals for laboratory trials. We housed the collected harvestmen in 20 × 10 × 15 cm terraria in a laboratory with a natural light regime (12 h/12 h) and continuous airflow. Each terrarium held 5 individuals of the same sex at a given time. We added fresh leaves and short branches for them to perch. We fed harvestmen with fruits, dry cat food, and dead insects once every day. Individuals were housed for 12 to 72 h before the trials.

### Experimental autotomy treatments

To experimentally test the effect of the loss of different leg types (locomotor and sensory) on mating behavior and the mating success of males, we experimentally induced autotomy in a subset of the eight-legged harvestmen collected in the field. For this, we held the animal by most of its legs and firmly held the base of the target leg's femur with forceps. Letting go of all legs except the target leg resulted in the individuals immediately releasing the leg. Autotomy was induced 1.5–2 h before the trials, which allowed us to control for the time since leg loss, and to ensure that their overall condition and behavior was unaffected (as done in Escalante and Elias 2021). Briefly, to quantify this we observed their movement, leg probing around the terrarium, and posture before and immediately after autotomy, as well as immediately before the mating trials.

We conducted 135 single-choice mating trials in which all females were eight-legged, but males varied in their leg condition. Our aim was to reflect the intensity of autotomy in

the field for this species. Of those trials, we excluded seven trials from the analyses because the harvestmen did not contact each other. Males were randomly assigned to three treatments: (1) males missing two locomotor legs (from pair I, Fig. 1) ( $n = 41$  trials), (2) males missing the two sensory legs (pair II, Fig. 1) ( $n = 43$ ), and (3) eight-legged sham control males, which we handled in the same way but without inducing autotomy ( $n = 44$ ) (Fig. 1). All individuals were used only once. In this population, 53% of 574 harvestmen were missing at last one leg (Escalante and Elias 2021). As for the type of leg missing, 22% of all individuals were missing one locomotor leg, 10% were missing two or three locomotor legs, 13% were missing one sensory leg, and 2% two sensory legs (Escalante and Elias 2021). We induced autotomy of locomotor legs I and not of legs III or IV, as the forelegs are used in sexual behavior, whereas hindlegs are not. Additionally, we chose these treatments to be consistent with the experimental design of our previous research that shows that losing two legs is the threshold for changes in locomotor performance (Escalante et al. 2020), oxygen consumption (Escalante et al. 2021), and habitat use (Escalante and Elias 2021). We thus consider that our experimental treatments allowed us to test for the effect of different types of autotomy on mating behavior and mating success.

### Mating trials

We conducted trials in transparent circular arenas (20 cm diameter, 30 cm high) with white paper as a substrate, as in Fowler-Finn et al. (2014). Females were acclimated to the arena for 5 min, and then, the male was placed in the arena. We recorded the interactions with a GoPro camera (HERO 4 Edition; GoPro, San Mateo, CA, USA) recording at 120 fps for later behavioral analyses. Trials were conducted between 19:00 and 0:00 h under dim red lights and lasted until copulation occurred (in which case we recorded the whole process) or 30 min passed.

The outcome of the trials was visually scored as: (a) no courtship, if the males did not display any courtship behavior after having had contact with the female. In Sclerosomatidae harvestmen, the courtship stage includes extensive tapping of the males as they contact the female, using their legs and pedipalps (the anterior pair of appendages, located between the mouth parts and the first pair of legs). Once both are in contact and in a face-to-face orientation, the male extends his mouthpart appendages (“chelicerae”) above the dorsal side of the female (Fowler-Finn et al. 2014). The male then attempts to hook his chelicerae to the basal segments of the female legs II (coxae) (Fowler-Finn et al. 2014). (b) Rejection, if the male courted and achieved chelicerae-coxal hooking but the female showed behaviors associated with rejection—the female lowered the proximal ventral side of her body to be in close contact with the ground, which

restricts mating (Fowler-Finn et al. 2014; Sasson et al. 2020, Classen-Rodríguez *unpubl.*). (c) Mating, when we observed intromission—penis insertion—(Fowler-Finn et al. 2014, 2018). We consider intromission a good proxy of fitness in these harvestmen (Macías-Ordóñez et al. 2010; Machado et al. 2015).

To further quantify the potential effects of autotomy on mating interactions, we extracted two behaviors from videos: (1) the length of the pre-copulatory interaction (hereafter referred to as ‘interaction’), measured as the time between the first leg contact and either a clear rejection from the female or the start of the genital intromission; and (2) mating length, measured as the time from the start to the end of the intromission, when the pair separated. Since our study involved observing two focal animals in a controlled setting, it was not possible to record data blindly.

### Morphological predictors of mating success

Variation in certain phenotypic traits influences sexual behavior and mating success in other North American *Leiobunum* harvestmen (Fowler-Finn et al. 2014, 2018, 2019; Sasson et al. 2020). To examine the influence of morphological traits, we measured the total length of the left leg I in males and females, the male pedipalp femur length, and the dorsal body area of both males and females (which was obtained by tracing the perimeter of each animal). With the latter two measurements, we calculated the female to male body area ratio to have a proxy for body size that incorporated size variation within the pairs. Measurements were done to the nearest 0.05 mm on preserved specimens (95% ethanol) using a camera attached to a dissection scope (Leica M205 FA), and measured using the Leica Application Suite software. We selected these morphological traits following previous studies (Fowler-Finn et al. 2014; Kilmer and Rodríguez 2017; Escalante et al. 2019).

### Data analyses

We tested for the effect of the male leg condition treatments on the outcome of mating interactions by performing a multinomial logistic regression. We used the trial outcome (no courtship, rejection, or mating) as the categorical response variable, and the leg condition treatment as a categorical predictor variable. The length of males’ leg I, the male pedipalp femur length, and the female/male body size ratio were included as continuous predictors. In this model, we also included the interactions between the predictor variables.

Given that we tested a null hypothesis of no effect, we calculated the effect size and the statistical power of the odds ratio of our comparisons (Cohen 1988; Nakagawa and Cuthill 2007). We made the three paired comparisons between the three experimental treatments (eight-legged

males, males missing locomotor legs, and males missing sensory legs). We compared the number of trials that resulted in mating relative to the sample size of each treatment. Then, we calculated the odds ratio and the  $r$  statistic from a contingency table (Nakagawa and Cuthill 2007) composed of the two treatments. We interpreted the effect sizes  $r$  of  $<0.20$  as small,  $0.21–0.80$  as medium, and  $>0.81$  as large (Cohen 1988; Nakagawa and Cuthill 2007). Next, we calculated the power ( $1-\beta > 0.95$ ) of each paired comparison as delineated in Rosner (2015). In addition to calculating these two parameters for our findings, we calculated the effect size and power of the difference size that our sample size would have allowed to detect. Comparing both scenarios, we were able to infer strong evidence for the absence of an effect.

We also tested the effects of the experimental male's leg condition on quantitative features of mating behavior. We ran one generalized linear model (GLM) with leg condition treatments as a predictor and the duration of pre-copulatory interactions as a response variable. We ran another GLM using leg condition treatment as predictor variables and mating duration as a response variable. Lastly, we ran a logistic regression using the duration of pre-copulatory interactions as a predictor variable and the trial outcome (interaction or mating) as response variable.

To control for potential between-treatment phenotypical variation, we ran three additional GLMs using leg condition treatment as the predictor variable and each morphological measure (male leg I length, pedipalp femur length, and female to body size ratio) as a response variable. Additionally, we ran correlation tests between the three morphological measures. All tests were run on R (Team 2019). The complete and raw dataset is available on [Dryad here](#).

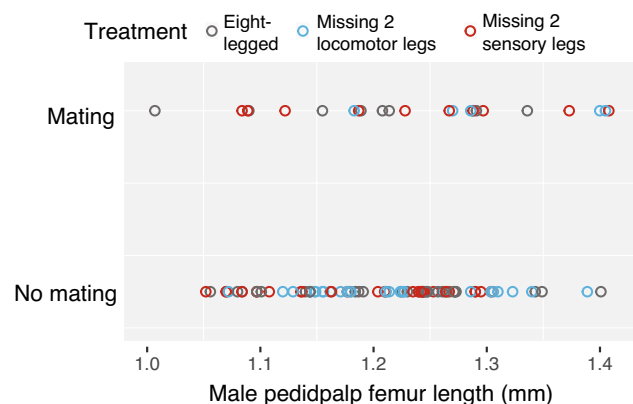
## Results

In the field, we observed 10 mating interactions that included all combinations of leg conditions (both eight-legged and autotomized males). In the laboratory experiment, the leg condition of males did not predict the outcomes of mating interactions (no courtship, rejection, or mating). Males missing locomotor or sensory legs were as likely to perform courtship as eight-legged males, and the rates of mating success were similar across the three leg condition treatments (20%, 17%, and 23%, respectively) (multinomial logistic regression: Estimate =  $-3.50 \pm 3.12$ ,  $P=0.91$ , Fig. 1). With our sample size (total  $N=135$  individuals), we had adequate power ( $1-\beta > 0.80$ ) to detect differences even of small size (e.g., effect size:  $r=0.20$ ). If we had observed differences between any of our groups, our estimate of effect size  $r$  as well as the statistical power to detect differences between treatments would have been low (eight-legged males and males missing locomotor legs:  $N=85$ , effect

size:  $r=0.04$ , power:  $1-\beta=0.054$ ; eight-legged males and males missing sensory legs:  $N=87$ , effect size:  $r=0.03$ , power:  $1-\beta=0.053$ ; males missing locomotor legs and males missing sensory legs:  $N=84$ , effect size:  $r=0.08$ , power:  $1-\beta=0.10$ ).

The outcome of the mating interactions was not predicted by the length of male leg I (Estimate =  $2.88 \pm 2.74$ ,  $P=0.29$ ), the male pedipalp femur length (Estimate =  $1.53 \pm 1.407$ ,  $P=0.27$ , Fig. 2), or the female/male body area (Estimate =  $8.99 \pm 1.05$ ,  $P=0.28$ ) (Table 1). None of the interaction terms of the models between leg condition treatments and the morphological measures were significant (treatment\*length of leg I: Estimate =  $4.07 \pm 5.29$ ,  $P=0.99$ , treatment\*pedipalp femur size: Estimate =  $1.47 \pm 2.58$ ,  $P=0.95$ , and female/male body area: Estimate =  $-1.97 \pm 1.65$ ,  $P=0.90$ ).

The experimental loss of different types of legs (either locomotor or sensory) had no effect on any measured feature of reproductive behavior. The duration of pre-copulatory interactions did not differ between treatments (Fig. 3), and was not affected by the male leg I length or the female/male body area (Table 2). Interestingly, we found a marginally significant trend that males with smaller pedipalp femur length were involved in trials with longer pre-copulatory interactions (correlation coefficient between pedipalp femur length and interaction length:  $r=-0.23$ , Table 2). Additionally, the mating duration did not differ between the leg condition treatments and was not affected by any morphological variable (Table 2, Fig. 3). Finally, whether the interactions resulted in rejection or in mating was not predicted by the duration of the pre-copulatory interaction (logistic regression: Estimate =  $0.014 \pm 0.013$ ,  $P=0.33$ ).

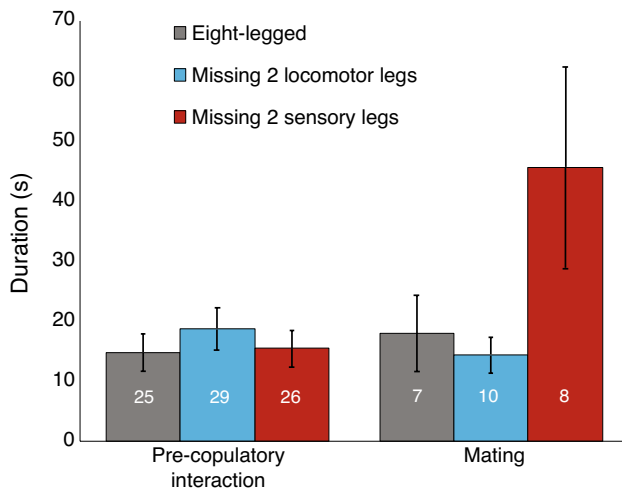


**Fig. 2** The male pedipalp femur length as a morphological predictor of mating success in the Neotropical *Prionostemma* sp.5 harvestmen in relation to the experimental leg condition in males. Pedipalp femur length did not predict if the mating trials resulted in mating or not (see 9 for further statistical details). This morphological feature did not differ between treatments (see 9)



**Table 1** Morphological measures of *Prionostemma* sp.5 harvestmen as a function of experimental leg condition treatment of males and trial outcome

			Male leg I length (mm)	Male pedipalp femur length (mm)	Female to male body area ratio
Experimental Treatments	Control	mean	59.6	1.19	1.82
		standard error (n)	0.42 (34)	0.02 (36)	0.04 (34)
		range	52.9—64.9	1.0—1.4	1.4—2.2
	Males missing 2 locomotor legs	mean	59.2	1.24	1.84
		standard error (n)	0.98 (13)	0.01 (33)	0.03 (33)
		range	53.2—66.8	1.1—1.4	1.3—2.2
	Males missing 2 sensory legs	mean	58.9	1.21	1.81
		standard error (n)	0.46 (30)	0.02 (35)	0.04 (31)
		range	52.0—62.9	1.1—1.4	1.4—2.2
Outcomes	No courtship	mean	59.8	1.21	1.83
		standard error (n)	0.54 (19)	0.02 (29)	0.04 (27)
		range	56.6—66.8	1.0—1.4	1.4—2.2
	Rejection	mean	59.1	1.22	1.81
		standard error (n)	0.46 (40)	0.01 (54)	0.03 (52)
		range	52.0—64.9	1.1—1.4	1.3—2.2
	Mating	mean	59.1	1.2	1.83
		standard error (n)	0.59 (18)	0.02 (21)	0.05 (19)
		range	52.9—62.1	1.1—1.4	1.4—2.2

**Fig. 3** Mean (+SE) durations of pre-copulatory and mating interactions in relation to the experimental leg condition treatment of *Prionostemma* sp.5 male harvestmen. Mean duration for either of these two behaviors did not differ among treatments (see 9 for statistical details). The sample size is shown inside each bar

We found no differences in the morphological measures between the male harvestmen of different leg condition treatments. The eight-legged, locomotor autotomy, or sensory autotomy treatments did not differ in the male leg I length ( $F_{2/74} = 0.45$ ,  $P = 0.64$ ), the male pedipalp femur length ( $F_{2/101} = 2.2$ ,  $P = 0.12$ ), or the female to male body area ratio

( $F_{2/95} = 0.37$ ,  $P = 0.66$ ) (Table 1). Moreover, those measures were not correlated with each other (leg I length and pedipalp femur length:  $r = 0.15$ ,  $P = 0.18$ , leg I length and size ratio:  $r = 0.16$ ,  $P = 0.19$ , and pedipalp femur length and size ratio:  $r = -0.07$ ,  $P = 0.51$ ).

The overall reproductive behavior (video S1) did not differ between eight-legged and autotomized males. All males performed behaviors such as leg and pedipalp tapping, coxal hooking, and leg grooming. However, we observed variation in the reproductive behavior between eight-legged males and males missing legs. For instance, males that lost locomotor legs performed the leg tapping courtship behavior with the remaining legs, and males that lost sensory legs did the leg tapping with legs I. Lastly, in two trials in which the outcome was rejection, the eight-legged male lost one locomotor leg of pair I during the courtship interaction with the female (however, it was not possible to observe what exactly caused it).

## Discussion

### Autotomy and reproduction in harvestmen

Our experimental findings provided support for the three predictions of the robustness hypothesis: the experimental loss of either locomotor or sensory legs in *Prionostemma* sp.5 male harvestmen did not affect their mating success

**Table 2** Statistical results of the models testing for the effect of losing different types of legs (experimental treatments) in males of *Prionostemma* sp.5 harvestmen on the pre-copulatory interaction length (s) and on mating duration (s) while interacting with eight-legged females

Variable	Parameter	Experimental treatments	Male leg 1 length (mm)	Male pedipalp femur length (mm)	Female to male body area ratio
Pre-copulatory interaction length (s)	Estimate	2.84	-0.3	-43.78	6.34
	Standard error	4.37	0.89	22.51	12.18
	<i>P</i>	0.51	0.74	0.057	0.605
Mating duration (s)	Estimate	28.95	-1.79	2.89	18.36
	Standard error	23.69	5.62	97.82	61.49
	<i>P</i>	0.25	0.76	0.97	0.77

(prediction 1) or any measured reproductive behavior (prediction 2). Additionally, autotomized males performed leg-related behaviors with different legs than eight-legged individuals (prediction 3). Our effect size estimates showed that we had adequate power to detect differences between the mating success of our experimental treatments. Therefore, we consider that our findings provide evidence of an absence of an effect of leg loss on mating success. Our laboratory data are supported by our field observations—we saw mating interactions of males and females that were missing legs. Altogether, despite the extensive use of appendages during courtship and mating in Sclerosomatidae harvestmen (Fowler-Finn et al. 2014, 2019, Classen-Rodríguez *unpubl.*), these arachnids are robust to variation in body form and show no negative consequences of leg loss in the fitness-related behaviors that we measured here.

We suggest that the costs of autotomy to harvestmen may not be as great as has been proposed for other taxa (Maginnis 2006; Fleming et al. 2007; Matsuoka et al. 2011; Emberts et al. 2019). Additionally, in a diverse range of animals it has been shown that individuals perform equally well or are easily able to adjust their behaviors to a modified body condition (DeWitt et al. 1999; Mikolajewski 2004; Kuo et al. 2015; Jagnandan and Higham 2017; Wilshin et al. 2018). Autotomized harvestmen of the same species we studied here showed no difference in survival in the field when compared to eight-legged individuals (Escalante and Elias 2021). Hence, our findings are in line with recent studies that suggest that robustness is prevalent in harvestmen. Future comparative work across this clade of harvestmen (as Burns et al. 2013; Burns and Shultz 2015, 2016; Kahn et al. 2018) should examine populations and species that show different levels of autotomy to test the robustness hypothesis.

### Losing different types of legs and plasticity

As predicted, losing legs (of any type) did not affect the mating success or mating behavior of *Prionostemma* males. Autotomized males showed plasticity in the type of leg used during pre-copulatory leg tapping behaviors. In another study, the loss of sensory legs affected the habitat use of

recently autotomized *Prionostemma* harvestmen, whereas the loss of locomotor legs did not (Escalante and Elias 2021). Additionally, losing two or more locomotor legs changed the proportion of locomotory gates used by individuals as potential strategies to escape predators (Escalante et al. 2020). Thus, while not affecting fitness, variation in body form does affect behavior and the ways that individuals move and interact with each other and with potential predators. Our results here then highlight that animals incorporate plasticity in order to compensate for bodily perturbations (i.e., bodily damage) (Emberts et al. 2019).

### Morphology, courtship, and mating

Variation in phenotypic traits in *Prionostemma* sp.5 males did not appear to affect the duration or the outcomes of mating interactions. We initially expected that males with smaller legs, pedipalps, as well as males with a smaller body size relative to females would have lower mating success, as observed in a variety of taxa (Morrell et al. 2005; Fowler-Finn et al. 2014; Wada 2017). However, only males with smaller pedipalp femur length had longer pre-copulatory interactions. While we predicted that pedipalp size would be target of sexual selection, our results suggest that the majority of phenotypic traits we measured are not targets of mate choice in this species. Interestingly, this is a novel finding for these arachnids, as body size predicted the likelihood of mating in some *Leiobunum* harvestmen (Fowler-Finn et al. 2014, 2018, 2019; Sasson et al. 2020).

### Robustness and the evolution of autotomy

Overall, our findings suggest that the evolution of autotomy as a defensive strategy is accompanied by traits that favor robustness. As autotomy evolved at least nine different times in animals (Emberts et al. 2019), it is reasonable to expect that some of those taxa might also have evolved multiple ways to withstand potential consequences of that bodily damage. This would allow animals to avoid experiencing the consequences of autotomy on critical behaviors such as courtship and mating that use body parts that

might be automatized. Selection on robustness for behaviors in other contexts is also likely. For instance, the ability to compensate for autotomy on locomotion likely drives the multiple mechanical, behavioral, and morphological compensatory mechanisms that animals use to mitigate the effects of leg loss (Jagnandan et al. 2014; Jagnandan and Higham 2017; Wilshin et al. 2018; Escalante et al. 2020). Other important behavioral contexts such as parental care, foraging, molting, and navigation are also likely robust and should be investigated.

### Crippling the study of autotomy and behavioral ecology

In the field of disability studies, the term *cripping* has been used to describe the act of deconstructing ‘mainstream representations [and] practices’ to bring to light assumptions about *able-bodiedness* and its exclusionary effects (Sandahl 2003; McRuer 2006; Barounis 2009; Hutcheon and Wolbring 2013). This field also focuses on how social constructions limit and foreclose the understandings of what *disability* and *able-bodiedness* are (Thomas 2007; Snyder and Mitchell 2010; Goodley 2016; Taylor 2017). Instead, they look to bodily variation and adaptability, ideas that resonate with the hypothesis of robustness we tested here.

In the study of autotomy, experiments are often interpreted through an *ableist* lens, as changes in behavior stemming from autotomy are assumed to be detrimental from a fitness perspective. We suggest an alternative approach that emphasizes the robustness of animals, as has been done in the field of biomechanics (Mongeau et al. 2013; Clark and Tribblehorn 2014; Jayaram et al. 2018) and systems biology (Kitano 2007; Félix and Wagner 2008; Nijhout et al. 2017). Across evolutionary time, animals encounter a variety of contexts that create variation in body forms and physiology (the *dis/ability* spectrum). We suggest that traits that increase survival across this spectrum will be favored and thus animals evolve to be robust, flexible, plastic, and resilient (able to recover to initial performance). Inspired by the field of disability studies, we suggest that our construction of fitness-related hypotheses is too limited to individuals that we perceive to be *intact* or *normal* and that our understanding of behavioral ecology suffers as a result. Autotomy provides a window into studying and understanding animal robustness in a variety of contexts. We suggest that the robustness of animals and behavioral strategies (and variation therein) across the *dis/ability* spectrum can be incorporated in how we think and theorize about organismal evolution and behavior. By doing so, we can better understand the variation of selective pressures in natural settings and how individuals respond given naturally occurring variation in behavioral strategies, traits, and conditions.

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**Authors’ contributions** I.E. and D.O.E. designed the study. I.E. collected and analyzed the data. I.E., and D.O.E. wrote the manuscript. Both authors read and approved the final version of the manuscript.

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**Availability of data and material** The complete and raw dataset is available on Dryad here ([https://datadryad.org/stash/share/4D-pEAFfmujk2qmgEnJc6Z\\_dc6p6fV\\_d1BcRDV8C60U](https://datadryad.org/stash/share/4D-pEAFfmujk2qmgEnJc6Z_dc6p6fV_d1BcRDV8C60U)). All individuals were deposited as voucher specimens at the Essig Museum of Entomology, University of California, Berkeley.

**Code availability** Not applicable.

### Declarations

**Conflict of interest** The authors declare no conflict of interest or competing interests.

Ethics approval.

This project followed institutional and national regulations for animal care.

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