

Territoriality evidenced by asymmetric intruder–holder motivation in an amblypygid



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ARTICLE INFO

Article history:

Received 4 September 2015
Received in revised form 1 November 2015
Accepted 17 November 2015
Available online 2 December 2015

Keywords:

Agonism
Asymmetric resource value
Contest
Motivation
Resource holding potential
Whip spider

ABSTRACT

Territoriality has an extensive and thorough history of research, but has been difficult to impossible to test empirically in most species. We offer a method for testing for territoriality by measuring the motivation of territory intruders to win contests in controlled trials. We demonstrated this approach by staging paired trials of the Amblypygi *Phrynos longipes* (Chelicerata: Arachnida). Amblypygids engaged in agonistic interactions after the opportunity to establish a putative territory on one side of an arena. We found that intruders of putative territories had lower motivation to win contests, thus evidencing territoriality. Physical components of individuals (i.e. energy stores) increased the probability of winning the contest for holders but not intruders, thereby providing insight into the differing decision rules opponents use in territory contests. We discuss why alternative hypotheses, including loser-initiator covariation and home field bourgeois advantage, fail empirical tests. We demonstrated that analyzing animal motivation in territorial contests is tractable even for animals where territories are inconspicuous and cues are outside the normal perceptions of researchers.

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1. Introduction

Territoriality occurs when animals defend spatially-associated resources against competing individuals (Marshall, 1996; Riechert, 1978). Territories are formed to defend food, mates, or refuges, often when they are limiting resources and patchily distributed (Maher and Lott et al., 2000). Animals communicate territory boundaries with signals, including those olfactory, auditory, vibrational, or visual (Pryke et al., 2001; Radford, 2003; Bowen et al., 2008). Territory signaling acts to reduce incidences of actual encounters by signaling individual resource holding potential (RHP), or the absolute fighting ability of an animal (Parker, 1974). The effect of territory ownership communicated by territory signals is measurable during agonistic contests—territory intruders are more likely to lose agonistic interactions than holders (Kemp and Wiklund, 2004; Bergman et al., 2007; Jennions and Backwell, 2008; Sacchi et al., 2009).

A hallmark of territoriality is that, all else being equal, territory intruders value the territory less than territory holders (Maynard Smith, 1974; Maynard Smith and Parker, 1976). This is most

commonly because there are costs for holders to attain a new territory and familiarity with a territory increases its value (Briffa and Hardy, 2013; Kokko, 2013). This effect is measured as variation in RHP. For example, Green hairstreak butterflies (*Chrysozephyrus smaragdinus*) intruding on an already established territory holder have lower RHP and are less likely to win contests than intruders (Takeuchi, 2006). RHP includes both motivation to win a contest (mRHP) and physical metrics like weaponry and body condition (pRHP). Thus, intruders should have a lower mRHP and be less likely to win territory contests than holders.

In a territory contest, mRHP (the component of RHP caused by motivation to win a contest), but not pRHP (the component of RHP caused by body size, weaponry, and energy stores), changes if an individual is the intruder or holder of a territory. This change in motivation is sometimes termed a residency effect (Kemp and Wiklund, 2004). If pRHP is accounted for, then the remaining difference in RHP between contestants is due to mRHP; an effect caused by territorial behavior. Thus, individual A has recognized the territory of B if, $RHP_A - pRHP_A < RHP_B - pRHP_B$, or $mRHP_A < mRHP_B$. That being said, mRHP and pRHP can interact to produce non-intuitive contest outcomes (Hårdling and Kokko, 2005; Parker and Rubenstein, 1981). For example, large individuals might have lower mRHP because there is little cost for high pRHP individuals to acquire new territories (Kemp, 2006). In this sense, mRHP is less important because total pRHP is much higher than the population

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average. Thus, mRHP \times pRHP interactions must be considered in interpreting territory effects.

Territoriality has been documented across most animal groups (Baker, 1983; Colwell, 2000; Maher and Lott, 2000; Reichert and Gerhardt, 2011) but often via abductive reasoning or anecdotal observation of territorial defense instead of empirical, experimental testing (Börger et al., 2008). Evidencing territoriality in animals has ranged from difficult to impossible because territorial behaviors remain inconspicuous and outside the regular perceptive abilities of researchers (Adams, 2001; Maher and Lott, 2000; Powell, 2000). Such is the case for species of the arachnid order Amblypygi. Amblypygids exhibit site fidelity (Chapin, 2014; Hebets, 2002) and agonistic interactions that follow stereotyped escalation (Fowler-Finn and Hebets, 2006; Weygoldt, 2000). While these observations point to territorial resource defense, territoriality has not been tested in any amblypygid species (Chapin and Hebets, 2016). This is no doubt in part due to their extraordinary sensory systems, communication modalities, and life histories, all of which seem alien to human researchers. Thus, we developed an empirical approach for testing territoriality in Amblypygi that is broadly applicable across taxa regardless of sensory modality and relies on established contest theory instead of abductive reasoning. In particular, we test for territory recognition evidenced by lowered motivational resource holding potential (RHP) of intruders informed by territorial cues.

We used the Amblypygi *Phrynus longipes* as a case study for our empirical approach to test for territoriality. Amblypygids are large, nocturnal, pantropical, predatory, and cannibalistic sister taxon of spiders (Giribet et al., 2002; Weygoldt, 2000; Wheeler and Hayashi, 1998). Amblypygids navigate with two elongate, antenniform front legs replete with sensory organs (Video 1–3; Santer and Hebets, 2008, 2009a). They employ olfactory (Hebets and Chapman, 2000), tactile (Santer and Hebets 2009a,b), and air movement signals (Santer and Hebets, 2011).

Amblypygids engage in aggressive but highly ritualized and stereotyped agonistic interactions when confronted with an opponent (Video 1–3; Weygoldt, 2000; Fowler-Finn and Hebets, 2006; Santer and Hebets, 2008) and seem likely candidates for territorial behavior (Weygoldt, 2000; Chapin, 2015). Contest outcomes for related species can be predicted by body size and agonistic displays (Fowler-Finn and Hebets 2006). Several species exhibit site fidelity, homing, and habitat preference (Chapin, 2011, 2014, 2015; Chapin and Hebets, 2016; Hebets, 2002; Hebets et al., 2014), all of which are associated with territoriality in other animals. Additionally, their life history hints at the need for a spatial resource worth defending: Amblypygids spend daylight hours in retreats to protect from daytime desiccation and predation. At night, they emerge and remain motionless to ambush prey (Weygoldt, 2000). Field research has shown that suitable retreats with available prey are oftentimes a limiting resource for amblypygids (Chapin, 2014). Although amblypygid agonism has been well studied relative to other areas of their biology, the function of agonistic interactions is unresolved and territoriality has not been tested (Weygoldt, 2000; Fowler-Finn and Hebets, 2006). Interpreting amblypygid interactions is challenging because they employ sensory modalities far different from those of humans. In particular, near-field communication (Santer and Hebets, 2008, 2009a) and complex olfaction (Hebets and Chapman, 2000) are used for intraspecific communication in the order. Thus, we tested amblypygid motivation to evidence for territoriality instead of more standard methods that would require measurements of territory signaling (Naguib, 2005), resources (Adams, 2001), or movement patterns (Atwood and Weeks, 2003).

We staged paired agonistic interactions of *P. longipes* to test for territoriality using the motivational and physical components of RHP. *P. longipes* agonistic displays involve tapping and vibrating with long antenniform legs and displaying and attacking with

Table 1

The $\bar{x} \pm$ SD and range of morphological measurements of *Phrynus longipes* considered for inclusion in models predicting the outcome of putatively territorial contests.

Measure	Range	$\bar{x} \pm$ SD
Maximum antenniform leg length (mm)	63.03–236.93	161.94 \pm 40.05
Maximum pedipalp femur length (mm)	3.08–18.82	10.94 \pm 3.34
Carapace width (mm)	6.36–19.04	13.77 \pm 2.89
Weight (g)	0.10–5.18	2.15 \pm 1.24
Scaled mass index	0.16–1.52	1.01 \pm 0.04

raptorial pedipalps (Video 1–3). These two agonistic “weapons” likely have distinct functions during interactions. Thus, we recorded weapon size in addition to contest outcome, residency, and body condition of the putative territory holders against intruders. We used scaled mass index (SMI) as a proxy for body condition of *P. longipes*. SMI is a superior estimate of body condition relative to mass-weight ratios or residuals because it accounts for the varying relationship of body mass and weight at different values of mass (Peig and Green, 2009). This measure incorporates energy stores given overall size, which are important for territorial contests (Marden and Rollins, 1994; Martínez-Lendeck et al., 2007; Peixoto and Benson, 2008). Overall body size alone can be a weak predictor of contest outcome in territorial disputes, especially for arthropods (Kemp and Wiklund, 2001; Peixoto and Benson, 2008). We designed a statistical model that included pRHP, mRHP, and their interaction and used an information-theoretic multimodel comparative approach to ascertain our prediction: *P. longipes* is territorial if putative territory holders and intruders exhibited asymmetric mRHP.

2. Methods

2.1. Study animals

In August 2012, we caught and measured *P. longipes*, held them individually for 24 h and then staged paired behavioral trials before their release. We collected animals between 1000–0400 h in August 2012 from Cueva de los Culebrones at Mata de Plátano Field Station, Puerto Rico generally located at 18.414°, –66.726°. Cueva de los Culebrones is replete with cracks and crevices used by amblypygids as retreats. As with most other amblypygids species, cave individuals were repeatedly found at the same retreat for weeks, and individuals would return to their same retreat after use in behavioral trials. For each animal, we recorded several morphological measurements as proxies for pRHP. We measured body size using maximum prosoma width and weaponry sizes as pedipalp femur length and antenniform femur length. Measurements were recorded using digital calipers to the nearest 0.01 \pm 0.03 mm. Additionally, we measured weight with a gram scale to the nearest 0.01 g. A summary of morphological measures is presented in Table 1. Following Peig and Green (2009), we calculated $SMI = M_i \times (M_x/W_i)^b$, where M_i and W_i are the total mass and maximum carapace width of individual i , M_x is the mean W of individuals, and b is the slope of an ordinary least squares log-log regression of M and W . We found that sexing by external structures was unreliable and instead sexed individuals by lifting the genital operculum after anesthetization via carbon dioxide gas. We recorded measurements at least 24 h before behavioral trials except for sexing via anesthesia, which we conducted after trials. Animals were housed separately in deli containers prior to trials for that 24 h period. We returned individuals to their capture site after experimentation. Animals that did not survive trials (due to occasional cannibalism) were preserved for further research.

2.2. Behavioral trials

Behavioral trials ($n=48$) were conducted in $75 \times 30 \times 30$ h cm glass arenas divided into two equal parts with a removable acrylic sheet (Video 1–3). We designed the arena to be large enough for individuals to move outside the antenniform leg-scanning zone (33.77 ± 9.25 cm dia.) of trial partners but small enough to encourage interactions. The arena floor was lined with unbleached paper to provide traction for movement. *P. longipes* cannot walk on glass, so animals were restricted to movement on the arena floor. We replaced paper and cleaned enclosures with isopropyl between trials. Territory recognition likely occurs via olfactory cues of opponents (Chapin and Hebets, 2016). Other research found that olfactory cues are used in individual-level recognition, and amblypygids have the physiology to detect a variety of compounds (Hebets and Chapman, 2000; Walsh and Rayor, 2008). Increased mRHP can occur just moments after territory acquisition (Bergman et al., 2007) and many territorial animals will engage in territory defense, even when relocated to laboratory conditions or otherwise unfamiliar areas (Fowler-Finn and Hebets, 2006; Tanner and Adler, 2009). Thus, we implemented an initial 10 min solitary period for animals to acclimate and potentially from territory cues after which we removed the divider to permit individuals to interact for 45 min. Since our analysis focused on the reaction of intruders, we were not concerned with the time territory holders needed to establish a territory. Instead, the reaction of intruders when faced with putative territory cues were of interest. We randomly selected captured individuals for inclusion in trials. Thus, contestant pairs included all size and sex combinations.

Behavioral trials were video recorded in darkness and at night under 940 nm peak wavelength infrared LED lights and a modified CCD camera with infrared bypass filter removed and fixed focus lens recording 640×480 p at 30 fps (Video 1–3). For each trial, we randomly chose one amblypygid to serve as the focal individual. We recorded whether this individual was the interaction initiator (i.e., oriented and began agonistic behaviors first), since contest initiation could interact with the contest outcome. Additionally, we recorded which side of the arena the focal individual was on at the start of the interaction; focal individuals were considered holders if the interaction started on their side of the arena, or intruders if not. Lastly, we recorded if the focal individual won or lost the contest by if it or its opponent ended the interaction by fleeing (i.e. orienting away from opponents or moving away from interactions). All behavioral data were recorded from video recordings of trials by one author (SLH) blind to project data to avoid inter-observer error and reduce bias.

2.3. Analyses

We included physical and motivational components of RHP, sex, and their interactions in a binomial generalized linear model to determine which, if any, predicted contest outcome. We used scaled mass index to represent pRHP. Antenniform leg length, pedipalp femur length, carapace width, and weight all correlated with SMI (Fig. 1), and were thus not included in model comparisons. We used residency (intruder or holder) as a measure of mRHP, and predicted that holders are more motivated than intruders. Thus, all else controlled, we predict that putative holders should win more often due to higher mRHP. Since RHP components can have interactive effects, we included interaction terms of predictor variables. Furthermore, we included sex as a predictive factor to account for potential differences in territoriality between the sexes. We compared the global model to more parsimonious versions via Akaike's Information Criterion corrected for small sample sizes (AICc) and Akaike weights (w_i). We tested parameters of the best model using Wald z -tests. We tested if males or females, and if intruders or hold-

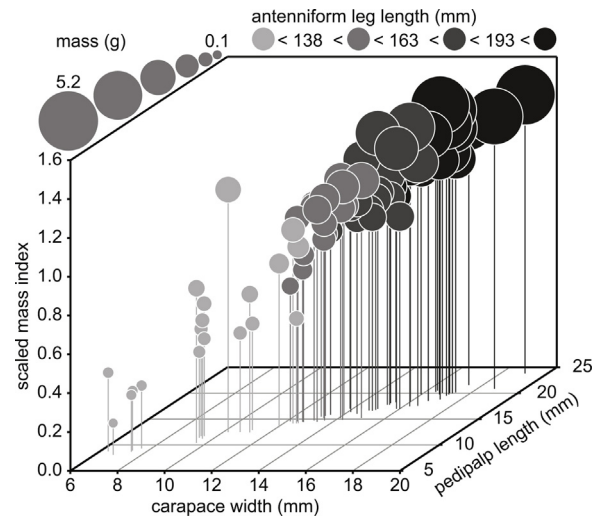


Fig. 1. Three-dimensional scatterplot illustrating collinearity of physical resource holding potential proxies for *Phrynus longipes*. Measures include scaled mass index, maximum carapace width (mm), and maximum pedipalp femur length (mm). Circle sizes represent antenniform leg length (mm) and circle color represents mass (g). A multivariate regression of all variables is strongly correlated (Adj. $R^2 = 0.88$, $F_{4,70} = 135.7$, $P > 0.0001$).

Table 2

Comparison of binomial generalized linear models predicting contest outcome in *Phrynus longipes*. The best model included the physical (scaled mass index; SMI) and motivational (residency) components of resource holding potential and their interaction. AICc is Akaike's information criterion corrected for small sample sizes; k is the number of model parameters (intercept included); Δ AICc is the difference in AICc of the i^{th} model and the lowest-scoring model; and w_i is the Akaike weight representing the conditional probabilities for each model.

Model	AICc	k	Δ AICc	w_i
SMI \times residency \times sex	114.65	12	12.52	< 0.01
SMI \times residency	102.13	4	0.00	0.51
SMI + residency	104.94	3	2.80	0.13
SMI	103.89	2	1.76	0.21
Residency	106.98	2	4.85	0.05
Intercept-only	105.37	1	3.24	0.10

ers, were more likely to win contests via χ^2 tests. Since contest initiators and holders could confound contest outcome, we tested if contests initiators were more likely to win contests using a χ^2 test.

3. Results

Agonistic interactions occurred in all trials ($n=48$) and followed a series of stereotyped, ritualized displays similar to other species (Video 1–3; Fowler-Finn and Hebets, 2006). Mean interaction time was 1.58 ± 0.30 min, and ranged from nearly instantaneous (i.e., immediately retreating after initial orientation) to up to 16.33 min. Multimodel comparisons indicated that the best model predicting contest outcome included SMI (pRHP), residency (mRHP), and their interaction (Table 2). Models with sex, without residency, or without SMI were worse at predicting contest outcome. Thus, both physical and motivational components of RHP affected contest outcome and intruders changed their behavior in response to the territory cues of holders. We confirmed this with post-hoc inference tests of best model parameters (Table 3). We plotted model estimates to illustrate interaction of SMI and residency (Fig. 2). High SMI improved the probability of winning contests for holders ($b=3.81$) but not for intruders ($b=-0.06$). Furthermore, residency (i.e., mRHP) increased the probability of winning contests among individuals with greater body condition.

Table 3

Model estimates and Wald tests for a binomial generalized linear model predicting contest outcome in *Phrynos longipes*. mRHP (residency), pRHP (scaled mass index; SMI) and their interaction are included in the model. Results indicate a significant interaction of SMI and residency.

Parameter	Estimate \pm se	z	P
SMI	-0.06 ± 1.08	0.054	0.957
Residency	-3.34 ± 1.94	1.73	0.084
SMI \times residency	3.87 ± 1.86	2.08	0.038

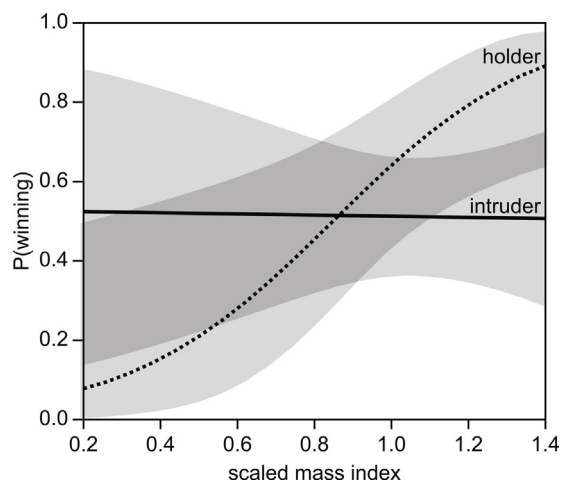


Fig. 2. Interaction plot of a binomial generalized linear model of residency (a measure of motivational resource holding potential; $b = -0.06$) and scaled mass index (a measure of physical resource holding potential; $b = 3.81$) predicting contest outcome for *Phrynos longipes* agonistic interactions. The dotted line represents putative territory holders and the solid represents intruders. Shaded areas indicate 95% confidence intervals.

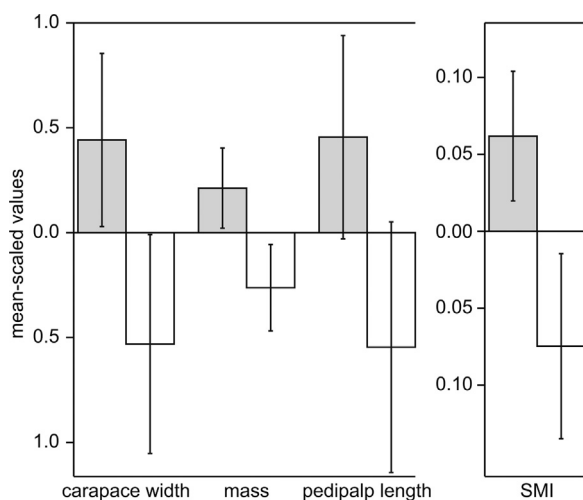


Fig. 3. Bar plot of mean-centered carapace width (mm), weight (g), scaled mass index, and pedipalp femur length (mm) of contest winners (grey bars) and losers (white bars). Lines indicate standard error of the mean.

Territory recognition is confirmed inferentially by a χ^2 test indicating that contests were 67% more likely to be won than lost by the holder ($\chi^2_2 = 7.26$, $P = 0.007$; $n = 88$ individuals). Contest winners had larger body size, weight, weaponry size, and SMI than losers (Fig. 3). We failed to detect if one sex was more likely to win contests than the other ($\chi^2_1 = 0.1854$, $P = 0.667$) which is in agreement with the unimportance of sex as a predictive variable in multimodel comparisons (Table 2).

We tested if these results were due to effects other than asymmetric mRHP, thereby discrediting the finding that the species is

territorial. Since holders and intruders are assigned by where the interaction occurs (i.e., either in one or the other's side of the arena), the case could be made that individuals that initiate interactions are more likely to both be intruders and lose contests (i.e., that the intruder-loser relationship is confounded by which individual initiates contests). We tested this by assigning an individual of each trial as the interaction initiator. We found that opponents that initiated the interaction were no more likely to win or lose than opponents that did not ($\chi^2_3 = 5.19$, $P = 0.16$) and were no more or less likely to be holders than intruders ($\chi^2_3 = 0.17$, $P = 0.98$).

4. Discussion

We found that *P. longipes* is territorial because contesting individuals displayed asymmetric mRHP, which interacted with pRHP. Intruders showed lower mRHP when in the presence of territory cues, indicating that intruders recognized the territory of their opponent and were less motivated to win the contest than holders. This held regardless of which individual initiated the contest. Put simply, individuals fought weaker when among the territory cues of another. Our research provides proof-of-concept results that intruder motivation is a measure of territoriality that can apply to animals with unobvious territorial behavior.

The mRHP \times pRHP interaction indicated that high pRHP improved the probability of winning for holders but not intruders. This result provides a glimpse into the different contest strategies in which holders and intruders engage. We posit that intruders always fight maximally against any holders regardless of pRHP, while holders hedge their bets in light of their own energy stores. Thus, holders enact a bourgeois-like, resource quality-dependent strategy when engaging in contests (Maynard Smith and Parker, 1976). This makes sense if, in the wild, territory holders have variable food stores while vagrants without territories fast until a new territory is acquired. Indeed, it is likely that a characteristic of high quality territories is proximity to food resources (Chapin, 2014). In keeping with this, holders with poor body condition may interpret their territory as equally poor, and therefore may not value it as much as holders with high body condition. Thus, amblypygids may use their own body condition as an indicator of territory quality. This corroborates to the lack of slope for intruders, which of course would not use their own body condition as a predictor of an opponent's territory quality. Thus, an intruder's probability of winning contests is unlinked with their body condition. The pRHP \times mRHP interaction indicated that holders should be more willing to give up territories if their body condition is poor, indicating poor territory quality.

An alternative explanation for increased holder mRHP is that familiarity with the space increases motivation (Kokko, 2013). A classic example is the home advantage in human sports competitions, where teams or individuals playing in familiar spaces (e.g., their home court) are more likely to win than rivals (Pollard, 2008). We argue that this is not the case with our study; we posit that gaining information about their side of the arena provides little advantage to holders, as there are no distinct physical features across arena sides. While it is unlikely that this effect influenced our study, territory holders in nature could benefit from this information. For example, holders may make better use of the spatial structures of their territory when engaging in agonistic interactions. Staging contests in structurally complex arenas may elucidate the effect this has on contest outcome.

Another alternative explanation is that the probability of individuals losing contests covaries with some other variable, such as which individual initiates the interaction. If initiating is correlated with a lower probability of winning contests, then an intruder-loser holder-winner pattern might explain our results. We tested

for this pattern and failed to detect a difference in the probability of contest initiators winning contests. We found that the observed pattern of territoriality and contest outcome was not explained by a correlation between losers and initiators. Animals that are more active were not more likely to be the intruder. Instead, contestants alter their mRHP based on their role (intruder or holder) in the interaction (Maynard Smith and Parker, 1976).

Territory effects have not been tested in any other Amblypygi species, but site fidelity seems pervasive throughout the order (Chapin and Hebets, 2016). Field research on three other Amblypygi species showed that individuals return to their capture site upon relocation and were found in the same location for repeated nights (Hebets, 2002; Hebets et al., 2014; Porto and Peixoto, 2013; Weygoldt, 1977). High quality territories likely attract mates, provide protection from predators and daytime desiccation, and are adjacent to the best foraging areas (Bloch and Weiss, 2002; Carvalho et al., 2012).

Olfaction is likely the primary mechanism for territory recognition in Amblypygi. Both physiological and ecological research on amblypygids has shown that olfaction plays an important role in amblypygid navigation (Hebets and Chapman, 2000). Indeed, olfactory cues were the only alteration to the arena available to opponents, and there exists no evidence of amblypygids altering their territory. Tactile perception is also important for amblypygids, but the arena did not offer tactile cues that would identify a territory (Hebets et al., 2014; Santer and Hebets, 2009b). Furthermore, at least one species of amblypygid has the ability to recognize individuals by olfactory cues (Walsh and Rayor, 2008). Given this, it seems likely that the short establishment period of our study is sufficient for individuals to engage in territorial defense; individuals in areas with olfactory cues of themselves behave like territory holders, while those among stranger olfactory cues behave like intruders. Holder behavior alone is not sufficient to explain the asymmetry in mRHP, because individuals often moved around the entire arena before engaging in contests. Indeed, our results show that holders that leave their putative territory and return to find an intruder are still more likely to win contests.

Territoriality has been hard to measure and test (Powell, 2000). One common measure of territoriality is to estimate to what extent home ranges are non-overlapping (Genovesi et al., 1997; Powell et al., 1996). This indirect method is limited to species with clear home ranges and that are amenable to long term, high resolution tracking. Another intuitive, but obviously challenging to execute, method is identifying territoriality by quantifying the costs and benefits of territorial behavior (Adams, 2001). Less common are field studies that manipulate home range spacing to test for residency. For example, spiders placed in artificial burrows close to territory holders were more likely to abandon their burrows (Moya-Laraño et al., 2002). This protocol is unfortunately intractable for most species and introduces asymmetry in resource quality. Our protocol does not require consideration of resource quality, or even the identity of the resource. Instead, we test the reaction of intruders to cues of a territory regardless if there is one, or if there is any reason to form one. Territoriality is evidenced by the response of intruders. This, however, should not imply that the type or value of the defended resource is unimportant. Species with conditional territoriality, in particular, require an understanding of resource value to replicate territoriality in the laboratory or examine animals in nature already in territorial behavioral states. Territory formation can depend on phenology, ontogeny, sex, phenotype, and resource abundance (Apio et al., 2007; Bibby and Green, 1980a,b; Johansson and Jonzén, 2012; Messier, 1985; Pröhl, 2005; Sinervo and Lively, 1996). An advantage of our assay is that, by repeated trials, it can identify the territorial season, sex, age, and environmental conditions for a species or population. For example, we showed here that *P. longipes* territoriality is not sex or ontogeny-

dependent—individuals responded to territory cues regardless of the sex or size of opponents.

We demonstrate an empirical approach to testing for territoriality by measuring motivation in putative intruders. mRHP evidenced territoriality. This method can address the challenge of testing for territoriality in species with less conspicuous territorial behaviors. Testing for territoriality via intruder mRHP can enable contest and territoriality research on a wider variety of taxa and conditions, thereby enabling further investigations into the diversity and functioning of territorial behaviors across Animalia.

Acknowledgements

This research was funded by the American Philosophical Society's Lewis and Clark Fund for Exploration and Research, UCLA's Edwin W. Pauley Fellowship, and the UCLA Department of Ecology and Evolutionary Biology Departmental Fellowship. Thanks to Eileen Hebets and Nonacs lab members for advice and feedback. Thanks also to field assistants Kimberly Dolphin, Chelsea Vretnar, and Daniel E. Winkler. Ingi Agnarsson, Heine Kiesbuy, and Armando Rodriguez provided logistics support. Research was conducted under the Puerto Rico Department of Natural Resources and the Environment permit number 2012-IC-064.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2015.11.014>.

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