

Seasonal resource value and male size influence male aggressive interactions in the leaf footed cactus bug, *Narnia femorata*



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ABSTRACT

In animal contests, resource value (the quality of a given resource) and resource holding potential (a male's absolute fighting ability) are two important factors determining the level of engagement and outcome of contests. Few studies have tested these factors simultaneously. Here, we investigated whether natural, seasonal differences in cactus phenology (fruit quality) influence interactions between males in the leaf-footed cactus bug, *Narnia femorata* (Hemiptera: Coreidae). We also considered whether males were more likely to interact when they were similar in size, as predicted by theory. Finally, we examined if male size relative to the size of an opponent predicted competitive success. We found that males have more interactions on cactus with high value ripe fruit, as we predicted. Further, we found that males that were closer in size were more likely to interact, and larger males were more likely to become dominant.

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1. Introduction

Males in many species compete for access to food, territories, and females (Andersson, 1994; Darwin, 1871). Contests may play out in a routine, stereotyped manner, increasing in intensity from displays to escalated physical battles. Yet, not all males compete, and many competitions do not progress beyond displays (Parker, 1974; Parker and Stuart, 1976; Smith and Parker, 1976). It may not be in an individual's best interest to engage with other males, as competing involves time and energy and comes with risks of injury and even death (Enquist and Leimar, 1990). Selection should favor individuals that use available information to determine when, and how intensely, to compete.

One important factor for the level of engagement is the perceived value of the sought-after resource (Arnott and Elwood, 2008). Previous work has provided mixed evidence on the extent to which variation in resource quality influences male–male competition, and further work is needed to determine to what extent different resource contexts alter levels and forms of engagement. In addition to resource value, resource holding potential should provide valuable information when deciding when and how to compete (Parker, 1974). Theory predicts that males of similar fighting prowess should be more likely to escalate competition, as the

expected outcome is less clear (Enquist and Leimar, 1983). In contrast, when fighting prowess is staunchly different, males with lower resource holding potential should avoid engagement after the initial assessment.

Here, we examine the effects of resource value and male size on male interactions in the leaf-footed cactus bug *Narnia femorata* (Hemiptera: Coreidae). *N. femorata* in North-Central Florida lives, feeds, and reproduces on the prickly pear cactus, *Opuntia mesacantha* ssp *lata*, (Majure, 2014), synonymous of *O. humifusa*; (Baranowski and Slater, 1986). Cactus fruit availability is especially important to this insect (Nageon De Lestang and Miller, 2009), but cactus fruit phenology and abundance vary seasonally (Cirino and Miller, 2017; Gillespie et al., 2014) and spatially (Cirino and Miller, 2017). Ripe cactus fruit provides multiple benefits during and after ontogeny; nymphs maturing on cactus with ripe fruit develop faster (Nageon De Lestang and Miller, 2009) and reach a greater size at adulthood than those spending part or all of their development on cactus pads without fruit (Gillespie et al., 2014; Joseph et al., 2016; Miller et al., 2016; Nageon De Lestang and Miller, 2009; Sasson et al., 2016). For *N. femorata* males, reaching a larger body size may be important to fitness because bigger individuals are more likely to win in male–male contests (Procter et al., 2012) and to be selected as mates (Gillespie et al., 2014). *N. femorata* males use hind legs for signalling and in physical engagement with rival males, as also occurs in other coreid species and in members of closely related families, (Eberhard, 1998; Fujisaki, 1981; Miller and Emlen, 2010; Mitchell, 1980; Miyatake, 1997; Okada et al., 2011; Tarnic and Spence, 2013). Body size is closely associated with hind

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femur size (weapon size) within Florida populations of *N. femorata* (Gillespie et al., 2014; Miller et al., 2016; Procter et al., 2012).

We capitalize on the ecology of *N. femorata* to examine the influence of natural, seasonal differences in cactus quality on male–male interactions. Based on the work of past game theory models (Enquist and Leimar, 1987; Smith, 1982), we predicted that males in high value, ripe fruit contexts would interact more than those in lower value contexts, cactus with unripe fruit or without fruit. Further, we test if males are more likely to interact when the size differences between males is small, as predicted by Parker (1974). Next, we test if male size relative to a competitor predicts dominance status. Previous work suggests that, overall, larger males in this species are more likely to be dominant (Procter et al., 2012), but no study in this species has tested the importance of male size in pairwise interactions. We use this opportunity to describe the fighting behavior of *N. femorata* to guide future work on male competition in this species and related species. For the purposes of hypothesis generation and future study, we also include a preliminary comparison of male courtship by, and female receptivity to, dominant and subordinate males.

2. Materials and methods

2.1. Insect rearing

We used laboratory-reared second and third generation *Narnia femorata* colonies in Spring 2014 and in Spring 2015 respectively. Seven wild-caught females and seven males were collected at the Ordway-Swisher Biological Station, Melrose, FL (29°41'N, 82°W), in September 2013, and used to establish the first lab colony. The founding parents of the second laboratory colony were collected as adults from the same site in September 2014, and kept as outbred lines for two generations; we used the offspring of eight different lines in this experiment.

The rearing protocol was similar in both years and for all generations. We kept colonies in a greenhouse during the early generations. Parental pairs (of the experiments insects) produced eggs in plastic deli cups containing a ripe cactus fruit and cactus pad potted in 1–2" of topsoil. We removed eggs from each adult pair and placed them in a separate container. We separated nymphs in their second instar into sibling groups of 5–10 per cactus pad per cup, as nymphs often aggregate in groups of this size in the wild. We reared these nymphs to adulthood in these cups in incubators which held the environment inside at 26° and 32° C (14 h light:10 h dark). We used the same growth chambers both years. We reared nymphs with variable temperature and nutritional exposure to simulate the variation in conditions these insects would experience if reared in the wild, randomizing each rearing group across all experimental treatments. We allowed the nymphs to mature to adults in these sibling groups, isolating them individually upon reaching maturity.

2.2. Competition observations

We observed male–male competitions when insects were 14–21 days adult, a narrow age-range selected to minimize the effects of aging on male–male competition and to test males soon after becoming sexually mature. We randomly assigned adult males to another adult male and a female (a trio) and did not pair siblings together. We assigned each trio to one of three competitive contexts: a potted cactus pad with one ripe fruit, a potted cactus pad with one unripe fruit, or a potted cactus pad without fruit. We evenly distributed these treatments across each day we performed trials. We observed 5–16 trios at a time, depending on the availability of eligible adult males on a given day. We conducted 58 trials from May to July 2014, conducting the remaining 36 in May 2015.

First, we introduced both males into a competitive context simultaneously to minimize resident/intruder effects, as are common in many species (Kokko et al., 2006; Parker, 1974). We allowed males ten minutes to acclimate to the environment. We next recorded male interactions for a two-hour period. Finally, we added a female to each pair of males to examine if female presence changed male–male competitive behaviors, as seen in amphibians, birds, and mammals (Cox and Le Boeuf, 1977; Montgomerie and Thornhill, 1989; Oda and Masataka, 1995). Existing work in this species has demonstrated that the selection on male size changes with the addition of a female (Procter et al., 2012), suggesting that males might fight or engage differently when a female is present. After introducing the female, we continued observations for another two-hour period, recording both male–male interactions and the male–female interactions for use in measuring mating success.

We conducted detailed observations in one of the two years (Spring 2014) to describe the male competitive behavioral repertoire for our focal insects. We found that males performed five distinct behaviors when paired with another male: (1) leg display, the raising of one or both hind legs in the line of sight of another male; (2) charge, a quick movement toward another male resulting in contact or withdrawal of the target male; (3) mount, climbing on top of another male; (4) kick, the use of one or both legs to quickly strike another male; (5) wrap, wrapping both legs around the body of another male. We also recorded (6) contact, any other physical encounter not falling into these categories. We recorded the number of instances within a trial each of these occurred, as well as the order in which they occurred in each trial, including whether they occurred before or after introducing the female.

2.3. Measuring competition and mating success

We determined dominance status by counting male withdrawal events. We defined withdrawal as whenever one or both males performed one of the six described competitive behaviors, followed by one or both males moving away from the other (Procter et al., 2012). We counted the male who first left the encounter as withdrawing, and scored both as withdrawing if both left. Scoring both as withdrawing ensured that we considered the encounter in the overall number of interactions, but did not increase or decrease either individual's dominance status. We scored the male who withdrew the least as the dominant male, and the male who withdrew the most as the subordinate. We had 4 incidences of equal withdrawals, and 60 incidences where male pairs did not interact during our observation period. We measured male engagement using two different metrics: a binary measure of whether or not males interacted and the count of the number of male interactions. We recorded mounting (climbing on top of a female) and male–female genital contact as measures of male courtship of females. We examined female receptivity to male courtship as a binary value, females that mated after genital contact (yes) and females that did not mate after genital contact (no). Females in this species must open their genital plates for a mating to occur, thus mating after genital contact is under female control.

2.4. Morphometric analysis

We froze males after completing each set of behavior trials. We took photographs of each individual with a Canon EOS 30D digital camera mounted on a dissecting microscope (Leica M165C). We used ImageJ (Schneider et al., 2012) to measure pronotum width of each individual. Previous work has shown that in this species pronotum width is highly correlated with body size (Gillespie et al.,

2014) and is thus used as a proxy for overall size in this species, e.g. Joseph et al. (2016).

2.5. Statistical analysis

We examined the influence of the pair's immediate environment on the number of male interactions per trial using a Generalized Linear Model (GLM) assuming a negative binomial distribution and logit link function. Our response variable was the number of interactions for each male pair ($n=94$), with the competitive environment (cactus without fruit, cactus with unripe fruit, and cactus with ripe fruit) as the predictor variable. We chose the negative binomial distribution because the majority of male pairs did not interact (60 out of 94 pairs) and over-dispersion made use of a Poisson distribution inappropriate.

We next tested whether males of similar sizes were more likely to engage in interactions than those male pairs more different in size. To do this analysis, first we calculated the percent size difference between males in a pair, and this number ranged from 0.01 to 23.7. We next ran a GLM with a binomial distribution and logit link function. Our response variable was whether males interacted or did not interact (0, 1) in their pair, and our predictor variable was the percent difference in male size of the males in the pair. We ran this GLM model and the previous in IBM® SPSS® V21.

Finally, we used an exact conditional paired logistic regression (Cox and Snell, 1989) in SAS Version 9.4 to examine whether larger male size predicted eventual dominance in male–male contests. For this test, we considered only male pairs where clear dominance was established (30 pairs out of the 34 that interacted). One male did not preserve well enough to measure size, so only 29 pairs could be included in this analysis. We considered male pairs as strata in this analysis, allowing us to examine success in relation to male size and the size of the specific competitor. This test specifically addresses the question of whether the larger male in a male–male dyad is more likely to become dominant.

3. Results

3.1. Male aggressive interactions

We first examined the influence of the pair's immediate environment on the number of interactions between males per trial and found that males on cactus with ripe fruit, the resource with the highest putative value, interacted more than those in the other resource contexts (Wald $\chi^2=8.377$, $p=0.015$; Fig. 1).

Next, we tested if pairs were more likely to interact when males were of similar size, and we found this to be the case (Binary GLM: Wald $\chi^2=3.994$, $p=0.046$; Fig. 2). Further, we found that the larger males in the pairs were more likely to become dominant (Paired logistic regression, Wald $\chi^2=1.4667$, $p=0.038$).

We found that 56% (19/34) of male pairs initiated and completed male–male interactions before females were introduced, while 17.6% (6/34) continued interacting with the female present, and another 26.4% (9/34) only began male–male interactions once the female was present. Male fighting behaviors revealed very few clear patterns, with the sequence of behaviors varying from trial to trial (Fig. 3). The presence or absence of females did not noticeably change the repertoire of behaviors males used in their contests. We observed that most behaviors had a similar rate of starting a contest, except for charges and kicks. Displaying legs and wrapping an opponent were the most common behaviors to occur and to settle a contest.

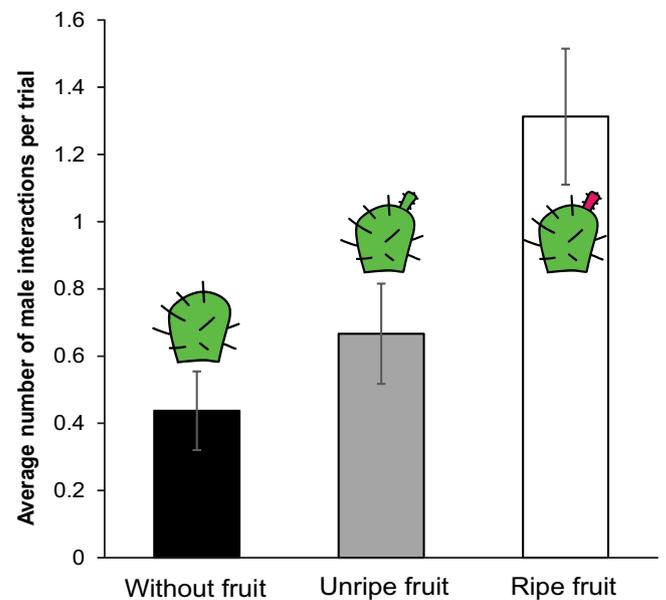


Fig. 1. Average number of male interactions per trial to each resource context. *Narnia femorata* male pairs were provided cactus pads without fruit, with unripe fruit, or with ripe fruit. We found that the number of male interactions was higher (\pm S.E.) as resource value increased, especially in high value, ripe fruit contexts.

3.2. Mating success

Descriptive statistics revealed that dominant males mated more often (50%; 15/30) than subordinate (20%; 6/30) or males from pairs where dominance was not established (20%; 6/30). Differences in mating by dominant males and subordinate males could be due to (1) females being more receptive to dominant males or (2) dominant males soliciting mating more than subordinate males. We found that dominant males established genital contact more often (63.3%–19/30) than subordinates (23.3%–7/30). There was no notable difference in mating success after genital contact across the categories (Dominant 78.9%, 15/19 versus Subordinate 85.7%, 6/7). Note that these descriptive statistics are only provided for the purposes of hypothesis generation and future study. These numbers reflect a randomly selected “focal” male from each container, because two males in a single container do not provide independent data points. Our sample size was not large enough to rigorously test these patterns.

4. Discussion

We found evidence that males in *Narnia femorata* use cues of resource quality, their size, and the size of their opponent when making decisions to engage in interactions. Competitions on higher value, ripe fruit resources saw more male interactions during our four-hour observation period. Males more closely matched in size competed more often than pairs with greater size discrepancy (Fig. 2). Further, larger males were more likely to become dominant in their male–male pairs. These results support our predictions and the expectations of game theoretical models that males will assess both the resource available and their opponent's fighting ability to determine their engagement in a contest (Enquist and Leimar, 1987; Smith et al., 1994). The trend of increased competition frequency and intensity with three-levels of resource value illustrates that males consider not just resource presence/absence, but also the level of resource quality, which has only rarely been documented (Arnott and Elwood, 2008).

Male competitive encounters in many species, including the coreid species *Leptoglossus australis* (Miyatake, 1993), feature an

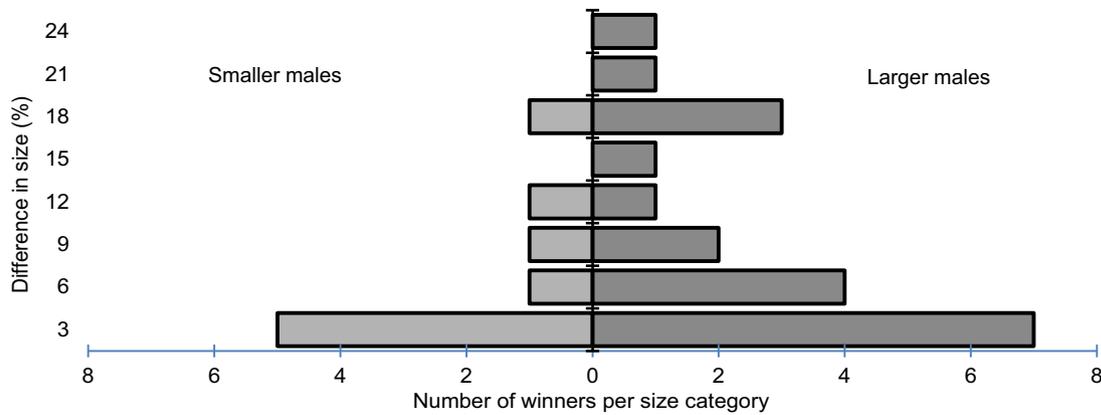


Fig. 2. Percentage difference in size to the number of contests won by larger or smaller males in pairwise contests. Size provides an advantage for *Narnia femorata* males in male–male contests. Larger males more often became dominant and more interactions occurred when males were similar in size.

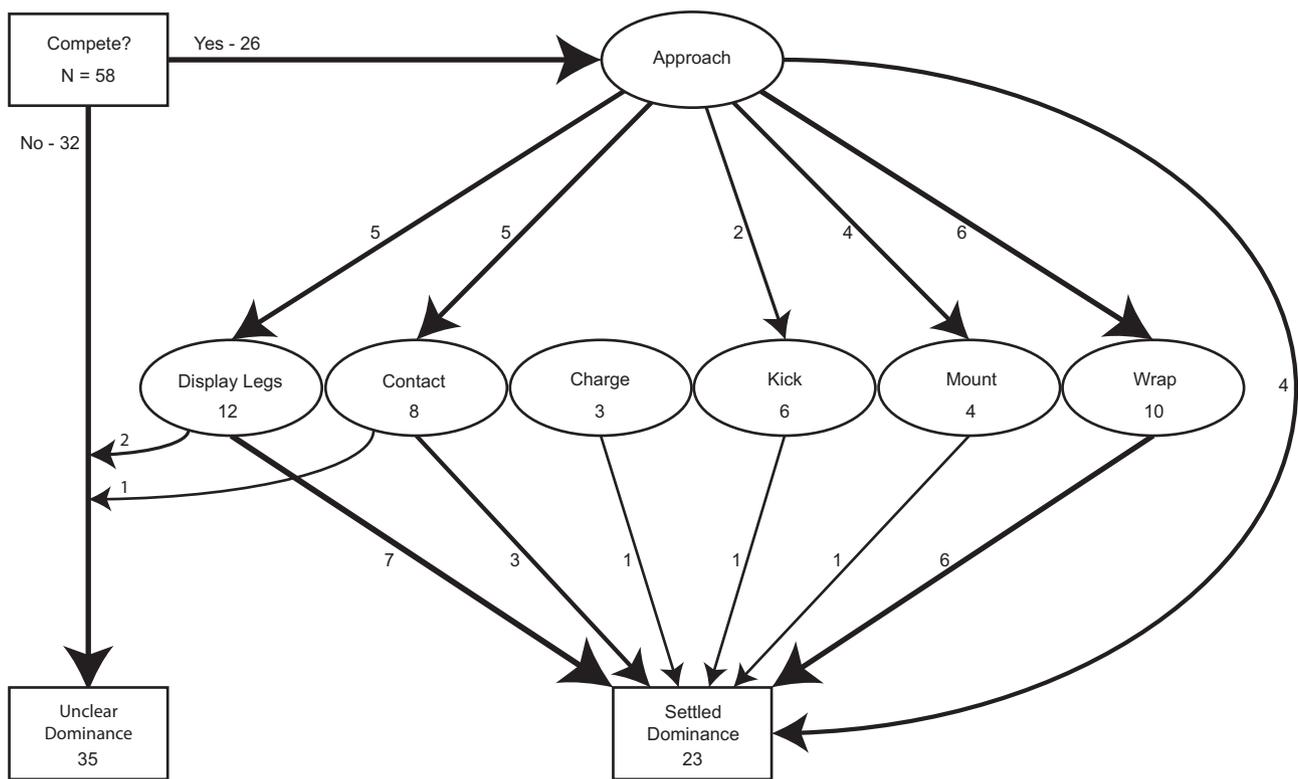


Fig. 3. Illustration of the path *Narnia femorata* competitions took during our 58 observations taken in 2014. The ovals represent discrete actions in a competitive encounter, with the number inside the oval corresponding to how many trials involved these actions at any point. Numbers and weighting of the arrows moving into the ovals represent how many competitive encounters began with these behaviors (charge does not have an arrow as no encounters began with a charge), arrows moving away represent the same for actions ending the encounter. Males who do not compete, or who do not establish dominance roles, were classified as unclear, and those that had clear dominance roles as settled.

escalation of behaviors in which males begin with putative low cost behaviors, moving to those of greater cost as an encounter progresses. In our four hours of observations, we did not find a clear escalation of behaviors, with males on average performing only one or two behaviors when competition occurred. Of these behaviors, low intensity leg displays, simple contacts, and high intensity wraps were the most common. The fighting behaviors are illustrated in Fig. 3 where we show the number of trials initiating with that behavior, the number of trials where we witnessed the behavior, and the number of trials where the behavior was the final one witnessed during the behavioral observations. Though we expected most males to initiate with a non-physical signal, such as the leg display, we found it was about as frequent as initiating with

the presumably costly wrap display, and it had a similar rate of determining the outcome of encounters. It may be the case that some presumably high-cost behaviors, such as the leg wrap and the mount, do not have as high cost as we expected, at least in the young and well-nourished males tested here. In the future, it would be interesting to test older males or those in poor physical condition for their body size to see if these findings hold. *L. australis* display escalated aggression behaviors when they are more closely matched in size; future studies in this species should size-match males of *N. femorata* to see if a similar pattern is found. Further, it will be useful to consider the likely use of pheromonal displays in the initial assessment period and throughout male engagement. Insects in this family often use pheromones to com-

municate (Aldrich and Blum, 1978; Leal et al., 1994; Prudic et al., 2008; Wang and Millar, 2000), though no existing study in this family has examined the use of pheromones in dominance interactions. Pheromones appear to be involved in male–male interactions in many arthropod species (e.g. Kortet and Hedrick, 2005; Moore et al., 1997). It would be fascinating to examine the role of pheromones in influencing the sequence of behaviors seen in Fig. 3 and the extent to which pheromonal production or quality scales with body size.

We added females to male pairs after two hours to determine if female presence changed the specific male–male competitive behaviors used, and it also allowed us to document mating behaviors by competing males. We did not detect a difference in the behaviors employed; yet, 26.4% of interacting males only began interactions once a female was present. Whether these interactions were initiated by the addition of the female or the length of time the males had spent together is currently unclear and warrants future study. We observed a greater number of mating attempts by dominant males than any other group, with similar rates of female receptivity. These results suggest that male status affects mating success, but not via female mate choice. Instead, dominant males may be more aggressive in seeking matings than subordinates, as seen in swordtails (Kingston et al., 2003). Alternatively, dominant males may prevent subordinate males from reaching females, as seen in trout and sticklebacks (Nilsson and Nilsson, 2000; Petersson et al., 1999). Our results on mating behaviors in a competitive context are intriguing, yet only preliminary.

Fighting in this species has a resemblance to fighting in other coreid species. Miyatake (1993) described four distinct fighting behaviors in *Leptoglossus australis*, “threat,” “combat,” “mount,” and “one-side attack,” the first three appearing to be directly equivalent to our observations of “leg display,” “wrap,” and “mount” respectively. Our “kick” appears to be similar to one type of “one-side attack” Miyatake (1993) describes, in which a male beats his competitor with one hind leg. We did not observe any behaviors similar to the other type of “one-side attack,” in which a male hooks and pulls his opponent by his forelegs, in any substantial measure. The wrap, or “combat,” behavior seen in these two studies has been observed in multiple other coreid species such as *Acanthocephala femorata* (Mitchell, 1980), *Acanthocoris sordidus* (Fujisaki, 1981), and *Acanthocephala declivis* (Eberhard, 1998). Enlarged, sexually-dimorphic hind legs and leg wrap behaviors are not limited to Coreidae, and have been observed in Alydidae (Okada et al., 2011; Suzaki et al., 2015) and Coleoptera (Eberhard and Marin, 1996). Males are typically the sex that fights, though females in *Leptoscelis tricolor* have been observed engaged in escalated contests involving leg wraps (C. Miller, pers. obs), and *Acanthocephala declivis* females are known to paw and swat at other females (Eberhard, 1998). Male fighting behaviors are associated with resource defense or female defense polygyny mating systems (e.g. *Acanthocoris sordidus*; Fujisaki, 1981). In some cases, territories are clustered in space, suggesting elements of lek defense polygyny (Eberhard, 1998; Miyatake, 1995) that may be best described as a “hidden lek” (Fletcher and Miller 2006). While species in the Coreidae and Alydidae share some commonalities in fighting behaviors, there are also intriguing differences that may correspond with variation in weapon shape and size. Further, many species across these groups have lost hind leg sexual dimorphism, and the species with monomorphic hind legs are not predicted to engage in aggressive physical contests. It would be fascinating to examine the evolutionary interplay between behavior and morphology across these groups in the future.

In conclusion, this study suggests that male *N. femorata* can accurately rank the quality of a resource and that this ranking influences the level of engagement with other males. We also found that males of similar size were more likely to engage in contests, evidence that males can assess themselves and their opponents.

Larger males were more likely to become dominant. Patterns of mating attempts and matings reveal that dominant males may be more likely to mate, not because of mate choice, but because they are more likely to engage with females. Future work on male–male competition in this species and others would benefit from considering factors such as the physical condition of males beyond body size (*sensu* Cotton et al., 2004); previous mating experience (Kendall and Wolcott, 1999); the immediate availability of resources in the surrounding area (Enquist and Leimar, 1987); and population composition and density (Cade and Cade, 1992; French and Cade, 1989; Greenfield and Shelly, 1985; Jirotkul, 1999).

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