

Original Article

# The relative importance of RHP and resource quality in contests with ownership asymmetries

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Ownership asymmetries lead to owners (residents) having substantial contest advantages over intruders, and this may overwhelm the fighting advantage of large body size. Why such an ownership advantage occurs, however, is not clear and requires further investigation. Here, we use a jumping spider, *Phidippus clarus*, to examine the role of ownership asymmetries and resource quality in determining contest outcomes and assessment strategies of both intruders and residents. Resident male *P. clarus* cohabit with and defend virgin females where reproductive potential increases with body size. Here, we show that ownership plays a significant role in contest outcomes, despite the previously demonstrated importance of body size when males encounter each other in the absence of a female. Owners have a substantial advantage over intruders with residency being more important than body size in determining contest outcomes. Intruders gave up more quickly when owners were larger, suggesting that owners follow a partial mutual assessment strategy. In contrast, contests won by intruders were “wars of attrition” where owners fought until resources were depleted as they were governed by the resource holding potential of the resident (loser). Finally, female size (reproductive potential) did not alter contest outcomes; however, it did affect how quickly contests were escalated. We highlight the importance of understanding the life history and reproductive biology along with the behavior and ecology of the species under study to truly understand the traits associated with fitness in contests. *Key words*: ownership asymmetry, owner advantage, resource quality, RHP asymmetry. [*Behav Ecol* 22:39–45 (2011)]

Contests are often settled through differences in resource holding potential (RHP) such that individuals with greater RHP win (Parker 1974; Parker and Rubenstein 1981; Enquist and Leimar 1987; Enquist and Leimar 1990). However, RHP dynamics are immediately altered as soon as one of the contestants takes an ownership role; owners are significantly more likely to win irrespective of RHP differences in many instances (Maynard Smith and Parker 1976; Maynard Smith 1982; Leimar and Enquist 1984; Mesterton-Gibbons 1992; Kokko et al. 2006). This is intriguing because several game theory models predict that the evolutionarily stable strategy (ESS) of either owner respect by intruders or intruder respect by owners (paradoxical ESS) is equally likely. Thus, in theory, owner and intruder are arbitrary roles and an arbitrary convention that determines contests outcomes (uncorrelated asymmetries; Maynard Smith and Parker 1976; Maynard Smith 1982) (but see Grafen 1987). The rarity of paradoxical ESS examples in real systems, however, suggests that asymmetries between contestants and resource quality are unlikely to be truly uncorrelated.

To examine effects of ownership on contest dynamics and outcomes, studies often use size-matched individuals to isolate effects of ownership alone (e.g., Beaugrand et al. 1996; Petersen and Hardy 1996). The empirical evidence from such studies is unclear, however, as such studies cannot distinguish whether owners winning is a by-product of 1) individuals with

an innately higher RHP aggregating as owners (e.g., Leimar and Enquist 1984; Kemp and Wiklund 2004), 2) ownership conferring some positional or physical advantage in contests (e.g., Stutt and Wilmer 1998; Fayed et al. 2008), and/or 3) ownership increasing the perception of the quality of the resource leading to owners fighting more aggressively (e.g., Bridge et al. 2000; Stokkebo and Hardy 2000). To truly understand the factors that are driving the evolution of ownership asymmetries requires taking into consideration differences in RHP and resource valuation and understanding the differences in contest dynamics that are relevant to the species under study (Kokko et al. 2006). Such examinations would provide a means to partition the relative importance of RHP, resource value, and ownership toward contest outcomes and to determine how these factors affect individual likelihood to initiate and escalate interactions. This is especially important as an ownership advantage may disappear at a point where an intruder's RHP advantage outweighs the benefits accrued by ownership, and this can further be affected by differences in resource valuation.

We used a species of jumping spider, *Phidippus clarus*, to examine the relative effect of RHP, ownership, and resource value on contest outcomes. During the early season, both sexes build hibernacula (nests) in curled leaves and return to these hibernacula each night (Hoefer and Jakob 2006). *Phidippus clarus* males mature first and search for and defend the hibernacula of penultimate instar females (one molt from maturity) (Hoefer 2007). On finding a penultimate female, guarding males build a hibernaculum immediately next to the female and fight rival males that attempt to displace them from their guarding position. As females mature almost simultaneously (within a 2–3 day window; Hoefer 2007), males are restricted to guarding a few or only a single female within

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a breeding season. Fighting is intense during this period as owners gain the opportunity to immediately mate with females after moulting.

Resident males commonly encounter roving males at female hibernacula (defended resource) as well as away from hibernacula, and fights are common in both scenarios. Males perform a series of stereotyped behaviors during aggressive interactions that have been described elsewhere (Elias et al. 2008). Briefly, these behaviors can be divided into 2 phases: 1) a precontact phase where males display toward one another and 2) a contact phase where males physically interact with one another. The precontact phase consists of visual and substrate-borne vibratory displays (Elias et al. 2008). The contact phase begins when the 2 spiders are close to each other and begin to leg fence. Leg-fencing behavior consists of the 2 males touching each other's horizontally outstretched legs whereby males attempt to push each other backward with their front legs and bodies. A subset of these interactions escalates to grappling. When roving males fight, size/weight predicts contest outcome (Elias et al. 2008), but it is not known how contests progress at hibernacula.

To examine the effect of ownership on contest outcomes in *P. clarus*, we exposed resident males (defending hibernacula with immature females) to randomly chosen intruding males, resulting in a distribution of size differences between owners and intruders. Such an experimental design allowed us to examine the role of ownership relative to RHP and the importance of resource quality in contest outcomes (Kokko et al. 2006). In addition to examining contest outcomes, we examined assessment strategies during the various contest stages using simple and multiple linear regressions according to Taylor and Elwood (2003) and Arnott and Elwood (2009). More specifically, we examined whether assessment strategies differed between contests where intruders successfully usurped owners and those where owners successfully retained ownership (e.g., Kemp et al. 2006). If intruders always respect owners, there should be no correlation between winner or loser RHP and contest dynamics because contests end before any evaluation occurs and/or resources are expended. In contrast, if intruders only escalate contests, which they can win, then according to the self-assessment that occurs in this species (Elias et al. 2008), loser (owner) RHP should correlate more strongly with contest dynamics than winner (intruder) RHP when intruders win (Taylor and Elwood 2003; Arnott and Elwood 2009).

There is evidence that males prefer larger females (Hoefer 2007), and the competitive superiority of larger males (Elias et al. 2008; Kasumovic, Elias, et al. 2009) results in size-assortative pairing (Hoefer 2007). This large female preference (Hoefer 2008) suggests that the value of the resource itself or the perceived value for each contestant may affect contest outcomes. Along with the variation in the quality of the resource, there may also be asymmetric knowledge of resource quality if owners have a greater opportunity to directly estimate the value of the resource they are defending (Enquist and Leimar 1987; Arnott and Elwood 2008) (e.g., Bridge et al. 2000; Stokkebo and Hardy 2000). Residents likely have superior knowledge of female value in *P. clarus* because hibernacula are small and intruders are attacked when approaching the entrance. If the quality of the resource affects contest dynamics or outcomes, we predict contest duration and likelihood of escalation to increase as the quality of the resource increases (i.e., a positive correlation between contest duration and female size). Furthermore, if there is asymmetrical knowledge of resource value, we predict that the value of the resource should only affect the behavior of the owner and that increased quality of the female should skew the RHP advantage associated with ownership toward the owner.

## MATERIALS AND METHODS

### Housing and competitions

We collected adult male and juvenile males and female *P. clarus* from Koffler Scientific Reserve at Joker's Hill, King, Ontario, Canada (lat 44°03'N, long 79°29'W), between June and August 2008. All individuals were housed in individual 3 × 3 × 5-cm clear plastic cages on a 12:12 h light:dark cycle and were fed small *Acheta domesticus* and *Drosophila hydei* twice weekly. Because jumping spiders are known to possess well-developed vision (Forster 1982; Land 1985; Land and Nilsson 2002), we ensured that cages were divided by opaque barriers to minimize the potential effects of prior visual interactions. All individuals were housed in this manner for at least 3 days to allow them to acclimate to laboratory conditions. We anesthetized males 2 days before trials using CO<sub>2</sub> and marked each individual with 2 spots of nontoxic fluorescent paint (Luminous paint; BioQuip Products, Inc., Rancho Dominguez, CA) on the dorsal part of the abdomen to allow individual identification during contests. These marks were not visible to contestants. We observed males during feeding intervals to ensure that males were not affected by the marking procedure.

We placed a small opaque rubber tube (1.5 cm in diameter and 4 cm long) within the cage of each penultimate female for use as a hibernaculum. Once females built a hibernaculum within the rubber tube, we moved females to a 10 × 10 × 3-cm plastic container and secured the tube within the center of the arena using blue tack. All 4 walls were covered with petroleum jelly to prevent individuals from climbing the walls. Females were allowed to acclimate to their new surroundings for a day after which we randomly placed a male within the container. We allowed a single day for males to acclimate to their new surroundings and build their own hibernaculum next to the penultimate female's hibernaculum. We only used pairs where the male was settled with the female, where both individuals were occupying their hibernacula within the tube, and where the female was verified as immature after the contest. We replaced any resident males that did not cohabit with another randomly chosen male after 1 day. New males were given a single day to cohabit.

To start each contest, we placed a randomly chosen male into the container and waited for the intruder to find the hibernacula. Males begin searching immediately and such handling does not affect contest outcomes (Elias et al. 2008; Kasumovic, Elias, et al. 2009; Kasumovic et al. 2010). The contest started once the intruding male reached the entrance of the opaque tube. Contests lasted until the losing male turned and ran from the winner, and the winner entered and settled within the tube. We timed all contests using a stopwatch, noting the time the individuals first observed one another, the time of first contact, the length of each bout, as well as the winner of each bout. However, as males begin displaying almost simultaneously and contests occurred within the opaque tube, it was difficult to observe which male initiated displays and contact. Thus, we could not directly examine motivation according to Kokko et al. (2006). However, we used the interval between the time when the opponents first observed each other and the first display or the time to first contact to examine the duration of each of the stages of the contest. We could unambiguously determine when the contestants had observed each other as both males remain motionless while directly facing one another before displaying. Additionally, we examined whether the contest escalated to contact phases.

After the contest ended, we removed each individual, weighed them, and placed them back into their individual cages. Females were reused in future fights for as long as they were immature. After all fights were completed, we digitally photographed each individual (Nikon Digital Camera DXM

1200) using a Zeiss microscope (Stemi 2000C). We then used Act-1 software to measure cephalothorax width (at its widest point) and the mean femur, patella–tibia, and tarsus of the first legs as measurements of size for males and only cephalothorax width for females.

### Statistical analyses

To first determine the traits important in contest outcomes, we performed a principal component analysis to remove the correlations between traits, resulting in 5 separate principal component axes that explained all the variation (see APPENDIX). This analysis demonstrated that the axis that explained the majority of variation in contest outcomes with ownership was the axis with a strong positive loading on male weight and a negative loading on other traits (see APPENDIX). As this result along with previous studies (Elias et al. 2008; Kasumovic, Elias, et al. 2009) demonstrated that weight is the most important trait predicting contest outcomes, we simplified our further analyses by using only weight as a descriptor of male RHP as this allows us to make biologically relevant comparisons between contestants.

We used the absolute difference in RHP between opponents (intruder – resident) to examine the role of RHP conventions in contest outcomes with ownership (Hardy and Field 1998). With the contest as the unit of analysis, we used a logistic regression with contest outcome as the dependent variable and absolute differences in RHP as the independent variable to examine the threshold size asymmetries required to balance residence asymmetries. We also used intruder-relative values ( $[\text{intruder} - \text{owner}]/\text{intruder}$ ) within a logistic regression to examine the relative value at which ownership no longer has an advantage because the relative advantage of ownership may vary depending on the size of the owner.

In a separate analysis, we examined the relative role of ownership and RHP in determining contest outcomes. For this logistic regression, we randomly selected a focal male from each pair and subtracted the opponent's weight to determine the weight difference. We then coded whether the individual was an owner or an intruder and whether the individual won the contest. This provided a secondary analysis that allowed us to determine the relative importance of ownership to RHP in determining contest outcomes. This analysis is comparable to a previous study examining the affect of experience and weight on the intermale contests that occur among roving males in this species (Kasumovic, Elias, et al. 2009). We also performed the same analysis as above but with mean standardized weight to allow comparison with previous studies.

We used 2 different analyses to examine whether the size (cephalothorax width) of the female altered contest outcomes. We first performed a multiple logistic regression with absolute weight difference between contestants as the independent variable, female size as a covariate, and whether the intruder won as the dependent variable. This model allowed us to examine whether the value of the resource (female size) shifted the resident advantage. In a second analysis, we used a multiple regression to examine whether the time to display, the time to contact, or contest duration were affected by the absolute differences in size (cephalothorax width) between each contestant and the female or the size of the female alone. This allowed us to examine whether the difference in size between the contestants and the female and the size of the female altered contest dynamics.

We used multiple and simple linear regressions to examine assessment strategies and contest dynamics according to Taylor and Elwood (2003) and Arnott and Elwood (2009). We first examined whether any aspect of contest dynamics was corre-

lated with the RHP of either contestant for all contests and then separately examined whether contest dynamics differed in contests where the owner retained ownership and where the intruder usurped the owner. We used a multiple regression to determine whether owner weight, intruder weight, and female size predicted contest duration. To examine how contest dynamics varied, we performed a multiple regression to examine whether contestant weights and female size affected contest initiation (time to first display) and a separate multiple regression to determine whether contestant weights and female size predicted the amount of time spent in the assessment phase (time to first contact) as 28 contests were settled without contact.

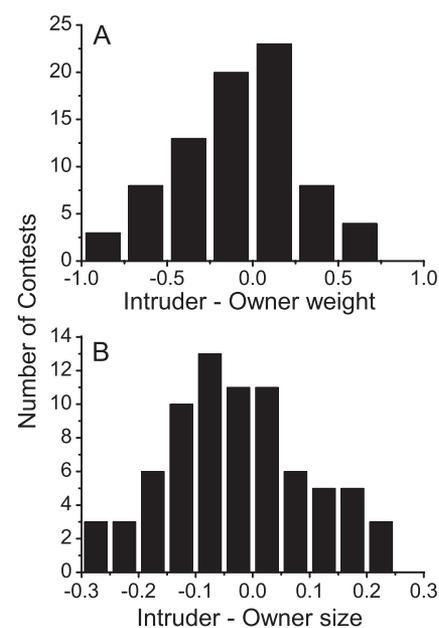
Statistical analyses were performed using JMP 7.0 (SAS Institute Inc., Cary, NC). We report standardized coefficients for  $\beta$  and adjusted  $r^2$  values.

## RESULTS

### Contest outcomes

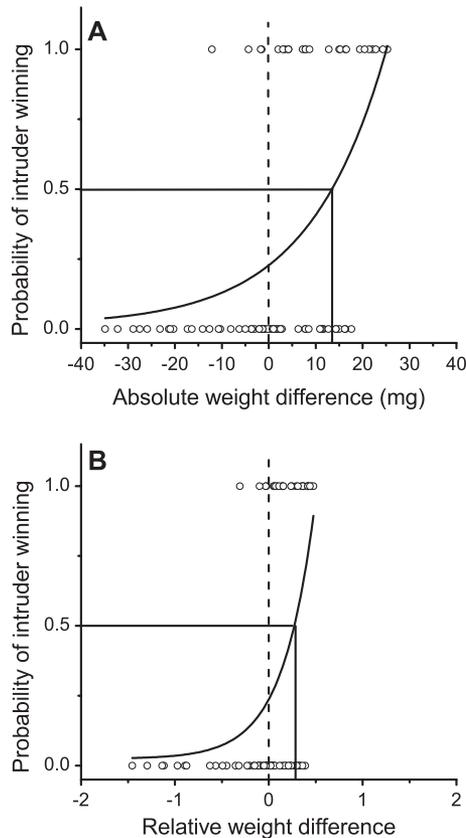
We observed a total of 76 contests with a normal distribution of absolute weight and size differences (Figure 1). During the experiment, 6 females were lost, resulting in 16 contests in which we could not measure the cephalothorax width of females. Thus, the samples size for examinations involving a female predictor variable was 60. All contests entered the assessment phase where individuals displayed toward one another; however, only 48 of the 76 contests further escalated to the contact phase.

RHP difference significantly predicted contest outcomes ( $\chi^2 = 19.04$ , degrees of freedom [df] = 1, 74,  $P < 0.0001$ ;  $\beta = -0.10$ ,  $r^2 = 0.198$ ). Owners thus had an equivalent of approximately a 12 mg weight advantage as demonstrated by the inflection point at which 50% of intruders won (Figure 2a). The same analysis using intruder-relative weight demonstrated that the ownership advantage disappeared when the intruder was approximately 25% larger than the owner ( $\chi^2 = 18.46$ , df = 1, 75,  $P < 0.0001$ ; Figure 2b) as



**Figure 1**

The distribution of (A) weight and (B) size (cephalothorax width) differences of male residents. Positive values signify heavier/larger residents, whereas negative values signify lighter/smaller residents.



**Figure 2**

Logistic regression of (A) weight difference (intruder – owner) and (B) intruder-relative weight (intruder – owner/intruder) difference as a function of contest outcomes. Dotted lines represent the point at which RHP is equal between contestants. Solid lines show the threshold point where the probability of winning is equal for both intruders and owners (i.e., above which the intruder's RHP advantage is sufficient to reverse the outcome of the contest in his favor).

demonstrated by the inflection point at which 50% of intruders won.

The secondary model using focal male weight differences with ownership as a predictor was significant ( $\chi^2 = 28.37$ ,  $df = 2$ ,  $73$ ,  $P < 0.0001$ ), demonstrating that ownership is the most significant predictor of contest outcomes ( $\chi^2 = 15.74$ ,  $df = 1$ ,  $73$ ,  $P < 0.0001$ ;  $\beta = 1.17$ , standardized  $\beta = 1.17$ ), followed by weight ( $\chi^2 = 19.18$ ,  $df = 1$ ,  $73$ ,  $P < 0.0001$ ;  $\beta = -0.10$ , standardized  $\beta = -1.44$ ).

### Female quality

Adding female size to the logistic model explained 0.19% more of the variation ( $\chi^2 = 15.51$ ,  $df = 2$ ,  $59$ ,  $P = 0.0004$ ); however, only male RHP difference significantly predicted contest outcome ( $\chi^2 = 10.24$ ,  $df = 1$ ,  $59$ ,  $P = 0.001$ ;  $\beta = -0.096$ ), whereas female size had no significant effect ( $\chi^2 = 0.004$ ,  $df = 1$ ,  $59$ ,  $P = 0.95$ ;  $\beta = -0.07$ ). There was no effect of female size or the difference in size between the female and either contestant on the time to display (all  $P > 0.17$ ) or contest duration (all  $P > 0.08$ ). The time to first contact was affected by the size of the female ( $F_{1,55} = 9.77$ ,  $P = 0.003$ ) and the difference in size between the resident and the female ( $F_{1,55} = 8.46$ ,  $P = 0.005$ ) with contests taking longer to reach first contact with larger females and when females were larger than the

resident. There was no effect of the difference in size between the female and the intruder ( $F_{1,55} = 0.88$ ,  $P = 0.35$ ).

### Contest dynamics

Intruders that usurped owners were generally significantly larger than owners (independent  $t = 4.86$ ,  $df = 74$ ,  $p < 0.001$ ), although this was not the case for all contests ( $N = 4$ ). There was no significant difference in the time to the first display ( $t = -1.35$ ,  $df = 74$ ,  $p = 0.18$ ), the time to contact ( $t = -1.22$ ,  $df = 46$ ,  $p = 0.23$ ), and contest duration ( $t = -0.19$ ,  $df = 74$ ,  $P = 0.84$ ) between contests where intruders won or lost. There was, however, a significant negative correlation between contest duration and intruder-relative weights ( $F_{1,74} = 7.64$ ,  $P = 0.007$ ). There was no correlation between intruder-relative weights and either the time to display ( $F_{1,74} = 0.57$ ,  $P = 0.56$ ) or time to contact ( $F_{1,46} = 1.44$ ,  $P = 0.24$ ). These results were quantitatively no different with the addition of female size as a covariate (results not shown here).

To determine whether contest dynamics differed when intruders won or lost, we performed multiple logistic regressions to examine contest dynamics separately for contests where intruders successfully usurped residents and where owners successfully retained ownership. We used female size as a covariate in these analyses to determine whether outcomes depended on female size. Neither intruder (loser) nor resident (winner) weight significantly predicted the time to display ( $F_{1,35} = 0.05$ ,  $P = 0.82$  and  $F_{1,35} = 0.21$ ,  $P = 0.65$ , respectively) or the contest duration ( $F_{1,35} = 1.08$ ,  $P = 0.231$  and  $F_{1,35} = 0.37$ ,  $P = 0.55$ , respectively) in contests where intruders lost. Female size also did not affect time to display ( $F_{1,35} = 0.0001$ ,  $P = 0.99$ ) or contest duration ( $F_{1,35} = 0.01$ ,  $P = 0.91$ ) in contests where intruders lost.

In contests where intruders won, although intruder (winner) weight was not correlated with time to display ( $F_{1,17} = 0.28$ ,  $P = 0.60$ ) or contest duration ( $F_{1,17} = 1.43$ ,  $P = 0.325$ ), resident weight (loser) was significantly positively correlated with the time to display ( $F_{1,17} = 6.25$ ,  $P = 0.023$ ) and contest duration ( $F_{1,17} = 4.52$ ,  $P = 0.049$ ). Female size did not affect time to display ( $F_{1,17} = 2.52$ ,  $P = 0.13$ ) or contest duration ( $F_{1,17} = 1.21$ ,  $P = 0.29$ ) in contests where intruders won. Performing the same above analyses except using simple linear regressions of the above variables according to Taylor and Elwood (2003) provided identical results and are therefore not shown here.

We used only contests that escalated to determine whether time to contact was significantly predicted by contestant weights and female size. Intruder weight ( $F_{1,26} = 0.002$ ,  $P = 0.96$ ), resident weight ( $F_{1,26} = 0.44$ ,  $P = 0.51$ ), or female size ( $F_{1,26} = 0.39$ ,  $P = 0.54$ ) did not significantly predict the time to contact in contests where the intruder lost. Resident weight ( $F_{1,12} = 10.71$ ,  $P = 0.007$ ) and female size ( $F_{1,12} = 6.45$ ,  $P = 0.027$ ) were significantly positively correlated with the time to contact in contests where intruders won, even though intruder weight was not ( $F_{1,16} = 0.02$ ,  $P = 0.88$ ). In simple linear regressions, the time to escalation was also only positively correlated with resident (loser) weight ( $F_{1,17} = 6.43$ ,  $P = 0.021$ ,  $r^2 = 0.23$ ) and not female size ( $F_{1,14} = 0.92$ ,  $P = 0.35$ ,  $R^2 = -0.005$ ) or intruder (winner) weight ( $F_{1,17} = 0.10$ ,  $P = 0.76$ ,  $r^2 = -0.05$ ).

### DISCUSSION

Male *P. clarus* respond aggressively to other males whenever they encounter one another in either a neutral setting or when roaming males encounter a guarding male. Previous research has shown that males use a mix of self-assessment and opponent assessment (partial mutual assessment; Prenter

et al. 2006) in determining contest outcomes in neutral settings (Elias et al. 2008). In such contests, weight is the only significant phenotypic predictor of contest outcomes (Elias et al. 2008; Kasumovic, Elias, et al. 2009), although previous experience also affects contest outcomes with prior contest winners being more likely to win (Kasumovic, Elias, et al. 2009; Kasumovic et al. 2010). Here, we show that ownership plays a significant role in contest outcomes and that although resource value does not affect contest outcomes, both the size of the female and the difference in size between the female and resident affected the time to escalation. Furthermore, we show that intruders are more likely to win contests when they have a higher RHP (i.e., are heavier).

Understanding why correlated asymmetries exist requires a careful examination of contest dynamics, player attributes, and an understanding of the behavior and ecology of the organism under study. Pure self-assessment or “war of attrition” game theory models (Mesterton-Gibbons et al. 1996) predict that contest duration is based on individual thresholds where individuals “give up” when these thresholds are reached. Contest dynamics are thus based predominantly on the individual that gives up first. Although we could not directly measure motivation because we could not observe which male initiated and escalated contests, we did examine how assessment strategies varied between contestants at different stages of a contest using multiple and simple linear regressions. This allowed a comparison of contest dynamics between contests where owners retained the resource and where intruders usurped residents to test whether RHP differences between contestants affect intruder behavior.

In contests where residents successfully defended the resource, no significant correlations with either resident or intruder RHP or female size were observed. Contests where residents won were not escalated more quickly, suggesting that residents were not more aggressive. Furthermore, as contest durations were not shorter when owners won, we provide no strong evidence of intruder respect. Contest duration for all contests, however, was significantly negatively correlated with the difference in weight between intruders and owners such that intruders gave up more quickly when owners were larger than them. We observed the same pattern if the analysis was completed separately for successful or unsuccessful intruders (data not shown). Thus, intruders did not seem to give up due to reaching their own limitations (self-assessment) or the quality of the resource but gave up because the resident was relatively larger (opponent assessment). In contests where intruders successfully usurped residents, we show that the first display and contest duration were significantly positively correlated with resident but not intruder weight. These results support a self-assessment strategy for owners as contest dynamics were predominantly driven by owner (loser) weight, suggesting that owners competed to their limit.

Our results thus suggest that contests with ownership asymmetries follow 1 of 2 trajectories. After an initial period of display and assessment, intruders abandon interactions with owners that are larger than them and retreat presumably to find other resources, thereby reducing costs associated with contests against potentially superior opponents. Although ownership allows direct access to virgin females in *P. clarus*, females mate multiply and wandering males may be able to secure some level of fitness with mated females later in the season, albeit at a decreased level (53% success rate; Sivalingham et al. 2010). Because lack of ownership does not preclude fitness, this has the potential to relax selection for ownership such that intruders should only escalate contests they are likely to win. In other instances, intruders engage in prolonged contests, which follow the rules of energetic wars of attrition (Mesterton-Gibbons et al. 1996).

This scenario suggests that intruders should only escalate contests, which they are likely to win (when they have a sizeable weight advantage; Figure 2), as resident males will fight to the limits of their reserves and such contests are likely to be costly. Our results thus suggest partial mutual assessment by intruders as they escalate contests where winning is more likely. In contrast, residents determine the amount of resources they will allocate to defending the resource (determined by the quality of the resource) and follow a self-assessment strategy, continuing to escalate until their resources are diminished.

In *P. clarus*, larger females are considered to be of higher quality as they produce more eggs (Hoeffler 2008). It is not surprising that resource quality did not affect how intruders behaved as intruders are attacked as soon as they reach the hibernaculum entrance. As a result, intruders would not have time to assess the resource and can thus only assess owners. Our results, however, suggest that residents also modify their behavior in response to the quality of the female. First, a larger difference between the size of the female and the resident affected the time to contact in all contests. Second, the time to contact was positively correlated with female size in escalated contests where intruders won. These results suggest that owners display for a longer period of time when females are larger and that resident males only give up when the benefit of retaining the resource outweighs the cost of further interaction. Our results thus agree with previous results, suggesting that size-assortative pairing in *P. clarus* occurs due to male preference for larger females combined with a competitive size advantage of larger males (Hoeffler 2008).

The strong ownership benefit that we demonstrated has the potential to alter life-history and fitness correlations throughout the breeding season (e.g., Härdling et al. 2004). For example, if residents have a 25% RHP benefit over intruders, maturing earlier may be beneficial even at the cost of maturing smaller as this allows rapidly developing males to secure a resource before later maturing males. Despite being smaller on average, the ownership benefit could allow males to maintain the resource. The strength of the ownership advantage should directly affect the importance and, therefore, the selection on maturing earlier (Vollrath and Parker 1992). This ownership advantage can further translate into an experience advantage if owners win their first contest (Kasumovic, Elias, et al. 2009; Kasumovic et al. 2010), which could result in selection for smaller males overall. Thus, it may pay developing males to determine the potential competitive challenges they are likely to encounter by assessing population densities and sex ratios (e.g., Zonneveld and Metz 1991; Wiklund et al. 1992; Kasumovic et al. 2008; Kasumovic, Bruce, et al. 2009) and alter their development in response to the detected competitive challenges (Kasumovic and Andrade 2006, 2009). This may occur in *P. clarus* because males constantly wander and have the opportunity to assess demographics using both visual and pheromonal modalities (Gaskett 2007). An ownership advantage can thus be added to the list of possible advantages for relatively smaller males (e.g., foraging advantage: Blanckenhorn and Viele 1999, mate searching advantage: Kasumovic and Andrade 2009, and functional temperature advantage: Moya-Laraño et al. 2007). However, there might also be a cost to ownership in this species; if weight is the significant predictor, then individuals that are guarding females may not have the opportunity to feed as often and may therefore decrease in weight compared with those that are searching for mates. This may decrease their RHP over time and, therefore, their ability to successfully defend females until they are sexually mature. Optimal male tactics may thus require balancing development time, adult size, and the timing and duration of mate guarding. We therefore highlight the importance of understanding the reproductive

biology and behavior along with the life history and ecology of the species under study to truly understand the traits associated with fitness.

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## APPENDIX

To determine which traits are most important in contest outcomes, we first standardized each trait and then used a principal components analysis (on correlations) to create 5 new uncorrelated axes that explained all the variation in phenotypic traits (Table 1). As some males did not have all measurements taken, this analysis was based on 140 males (70 contests). The first axis (PC1) described overall size with all traits loading approximately equally (Table 2). As the loadings of each of the 5 traits varied for the remaining 5 axes (PC2–PC5) (Table 2), these axes described overall variation in shape. We used the absolute difference in PC scores between opponents (intruder score – resident score) to examine the role of each of the axes in explaining variation in contest outcomes with ownership (Hardy and Field 1998).

With the contest as the unit of analysis ( $N = 70$ ), we used a backward stepwise regression with contest outcome (whether the intruder won) as the dependent variable and the absolute differences in the 5 PC scores as the independent variables. Of all the axes, only PC1 ( $\chi^2 = 3.39$ ,  $df = 1$ ,  $67$ ,  $P = 0.066$ ) and PC3 ( $\chi^2 = 3.62$ ,  $df = 1$ ,  $67$ ,  $P = 0.057$ ) were near significance. We then performed a logistic regression with only these 2 principal components to examine the significance. Only PC3 significantly explained the variation in contest outcomes ( $\chi^2 = 3.63$ ,  $df = 1$ ,  $67$ ,  $P = 0.048$ ), and PC1 was nearly significant ( $\chi^2 = 3.39$ ,  $df = 1$ ,  $67$ ,  $P = 0.066$ ).

Examining PC3 demonstrates a strong positive loading of male weight with mainly negative and weak loadings of other phenotypic traits (Table 2). Along with the near significance of PC1 where all traits loaded approximately equally, these results suggest that although overall size is important in contest outcomes, relatively heavier males are more successful. To simplify our further analyses and to allow biologically relevant comparisons, we thus only used weight as the determinant of male RHP.

**Table 1**

**The eigenvalues and the amount of variation explained by each of the principal component axes**

PC axis	Eigen value	Percent	Cumulative percent
PC1	4.390	87.80	87.80
PC2	0.253	5.06	92.86
PC3	0.186	3.71	96.57
PC4	0.121	2.42	98.99
PC5	0.050	1.01	100

**Table 2**

**The loadings of the 5 traits on each of the principal component axes**

	PC1	PC2	PC3	PC4	PC5
Weight	0.44448	-0.07390	0.73531	-0.50397	-0.04801
Cephalothorax width	0.45072	-0.23014	0.26687	0.82015	0.00509
Femur length	0.45735	-0.29157	-0.40134	-0.20696	0.70846
Patella–tibia length	0.45729	-0.24108	-0.45966	-0.16503	-0.70303
Tarsus length	0.42546	0.89355	-0.12543	0.05750	0.03883

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