Quadratic resource value assessment during mantis shrimp (Stomatopoda) contests

Green, P.A.[1, 2*] & Harrison, J.S.[1]

[1]Biology Department, Duke University, Durham, NC 27708, USA

[2]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn, Cornwall TR10 9FE, UK

[*]Corresponding author email: p.a.green@exeter.ac.uk; phone: +1 530-417-2089;
mailing address: University of Exeter, Centre for Ecology and Conservation, Stella Turk
Building, Treliever Road, Penryn, Cornwall TR10 9FE, UK

HIGHLIGHTS

- Mantis shrimp inhabit protective coral rubble burrows in a size-assortative manner.
- Intruders without burrows won fights over burrows smaller than the predicted ideal.
- Intruders won by delivering more high-force strikes and by being aggressive first.
- Burrow residents showed no evidence of burrow size assessment.
- The quadratic resource value assessment we describe may inform other systems.

ABSTRACT

Resource value assessment—in which competitors adjust behaviours according to the perceived value of a contested resource—is well-described in animal contests. Such assessment is usually assumed to be categorical or linear; e.g., males fight more aggressively when females are present than absent, or as female fecundity increases. Here, to our knowledge for the first time, we show quadratic resource value assessment, in which resource value is highest at a certain level and decreases in either direction. The mantis shrimp *Neogonodactylus bredini* occupies coral rubble burrows in a size-assortative manner: individuals of a certain body size inhabit burrows of a certain size. Using mock burrows of various sizes, we tested whether mantis shrimp 1) chose burrows predicted to be best fit for their body size, and 2) were more aggressive during, endured higher costs during, and were more likely to win, contests over burrows predicted to be best fit. Individuals chose burrows larger than their predicted best fit burrows. In contests, intruders without burrows were more likely to evict burrow residents when the burrow was slightly smaller than the intruder's predicted best fit size. Intruder success decreased as relative burrow size increased or decreased from this value. Intruders won by delivering more strikes and by being aggressive first. In contrast to intruders, burrow residents showed little evidence of resource value assessment. A literature review revealed that quadratic resource value assessment may play a role in contests over resources from territories to parasite hosts. Therefore, our results impact theoretical models of contest behaviour and may lend insight to how contests affect resource distributions.

KEY WORDS

Animal contests; assessment; mantis shrimp; resource value; resource ecology

INTRODUCTION

Competing animals may gather information about, or assess, fighting ability, which competitor owns a contested resource, and how competitors value a contested resource (reviewed in Hardy & Briffa, 2013). How animals assess these factors determines variation in contest behaviours and outcomes. Therefore, assessment of fighting ability, resource ownership, and resource value can each influence the evolution of contest behaviours (e.g., birdsong, reviewed in Searcy & Beecher, 2009) and structures (e.g., weaponry, reviewed in Emlen, 2008), as well as how individuals and resources are distributed (e.g., monopolizing mates, Clutton-Brock, Albon, Gibson, & Guinness, 1979). Assessment of own and/or opponent fighting ability, termed resource holding potential (RHP) by Parker (1974), is perhaps the best-studied factor influencing contest behaviours and outcomes. RHP is generally determined by size metrics like body mass (Briffa et al., 2013; Vieira & Peixoto, 2013). All else being equal, the contestant with greater RHP is predicted to win (reviewed in Arnott & Elwood, 2009). Resource ownership effects have also been well-studied: resource owners typically win contests, even if at an RHP disadvantage (reviewed in Riechert, 1998). Here, we focus on how resource value assessment can influence contest behaviours and outcomes.

Theory predicts, and empirical tests often find, that competitors assess the value of a contested resource and adjust their behaviour accordingly, with corresponding changes in the likelihood of contest success (reviewed in Arnott & Elwood, 2008). For example, female parasitoid wasps (*Eupelmus vuilleti*) compete over hosts in which to lay their eggs. High-quality (e.g., larger) hosts represent more food for a female’s young and, as a female’s egg load increases, she must rapidly find a host for her eggs. Therefore, host quality is a resource assessed during contests over hosts, and a female’s assessment of host quality may be affected by her egg load. A. G. E. Mathiron, Pottier, and Goubault (2018) found that, in contests over high-quality hosts, females raised in poor environments fought more aggressively and were more likely to win than females raised in good environments. Females with more eggs than their opponents were also more likely to win (A. G. E. Mathiron et al., 2018). These results show how assessment of resource value—both the objective value (size) of the host and the subjective value of the host to females from different developmental backgrounds and with different egg loads—affects the behaviours competitors use and the outcomes of contests.

Studies of resource value assessment like that described above for parasitoid wasps have a long history in the field of contest behaviour (reviewed in Arnott & Elwood, 2008). These studies have overwhelmingly tested resource value effects in either a categorical (e.g., good or poor environment) or linearly increasing (e.g., number of eggs) fashion. Indeed, a survey of papers cited by, and that have cited, a seminal review of resource value assessment (Arnott & Elwood, 2008) found that all studies have tested either categorical or linear effects (Table A1). An alternative to this categorical or linear assessment is quadratic resource value assessment, in which the value a competitor places on the contested resource peaks at some level and decreases in either direction from this peak. Here, we test for quadratic resource value assessment in a burrow-dwelling mantis shrimp.

Quadratic resource value assessment has been implied, but to our knowledge not explicitly tested, in previous studies. For example, the hermit crab *Pagurus bernhardus* occupies snail shells in a size-assortative manner: for crabs of a given size, smaller shells function poorly in predator defence while carrying larger shells imposes energetic costs (reviewed in R. W. Elwood & Briffa, 2001). Studies of resource value in this system have found that contest aggressive behaviours, contest costs (e.g., duration), and contest outcomes vary according to categorical (e.g., larger, smaller, or the preferred shell size, R.W. Elwood & Glass, 1981; Doake & Elwood, 2011) or linear (i.e., the absolute value of the difference between contested shell size and preferred shell size, Hazlett, 1978) variation in shell size (see also Table A1). While these studies clearly show that hermit crabs assess resource value, by imposing categorical or linear effects on what might be a quadratic relationship they may obscure nuanced information regarding the selective forces influencing contests. For example, energetic costs may be less important to competing animals than predation risk (Riechert, 1998, 1988). For hermit crabs, the energetic costs of carrying a slightly larger shell may be low compared to the predation risk imposed by carrying a slightly smaller shell. If this were the case, resource value might be high for both preferred shells and shells slightly larger than preferred, with resource value decreasing as contested shells become larger (higher energetic cost) or smaller (higher predation risk) than this peak. Quadratic resource value assessment may also occur in other systems, for example in territorial species with varying levels of experience on their territory (Krebs, 1982), or when males compete over females whose fecundity rises then falls over the lifespan (Stokkebo & Hardy, 2000).

Here, we test for quadratic resource value assessment in the mantis shrimp *Neogonodactylus bredini*, a species in which both sexes compete over access to burrows in coral rubble (Caldwell & Dingle, 1975). *N. bredini* exchange potentially damaging, high-force strikes during these contests in a ritualized behaviour (Green & Patek, 2015) that facilitates mutual assessment of body mass, a metric of RHP (Green & Patek, 2018). In Panamanian seagrass beds, *N. bredini* population density is limited by burrow abundance, and the volume of inhabited burrows is strongly correlated ($R^2 = 0.78$) with the body length of burrow residents (Steger, 1987). Burrows function as protection from predation (Berzins & Caldwell, 1983), a place to mate (Caldwell, 1991) and brood eggs (Montgomery & Caldwell, 1984), and a place to safely moult (Caldwell, 1987). A close match between burrow volume and mantis shrimp size might be important, for example, because mantis shrimp use their armoured tailplate (“telson”) to block the burrow entrance from predators and competitors (Taylor & Patek, 2010). To gauge burrow size, mantis shrimp may use visual, tactile, or other sensory modalities (Reaka, 1980). Given the importance of burrows to mantis shrimp biology, and because they inhabit burrows in a size-assortative manner, we hypothesized that competing mantis shrimp would assess resource value in a quadratic fashion. That is, a mantis shrimp of a certain body length would place highest value on a burrow of a certain volume and lower value on burrows larger or smaller than this “ideal” volume. This hypothesis predicts that mantis shrimp would be more likely to win, be more aggressive during, and endure higher costs during contests over burrows of the ideal volume. Further, it predicts that contest success, aggression, and costs decrease as burrows change in size from the ideal.

We tested this hypothesis using mock burrows of known volume in choice experiments and staged contests. In choice experiments, we tested the prediction that individuals would preferentially choose mock burrows closest to the ideal natural volume for their body size based on *in situ* data (Steger, 1987). In staged contests, we paired competitors in contests over access to mock burrows in which competitors were randomly matched with respect to each other’s body mass and to the volume of the contested burrow. We predicted that competitors would be more likely to win, would show more aggressive behaviours, and would have costlier (e.g., longer) contests when their body lengths were an ideal match for the volume of the contested burrow. We predicted that contest success, aggression, and costs would decrease as the match between competitor body length and burrow volume changed from the ideal.

METHODS

A schematic of the experimental process is shown in Fig. 1.

Mock Burrow Design

We built 11 sizes of mock burrow that evenly spanned the variation in natural burrow volume measured by Steger (1987). Burrows were made of clear plastic tubing with only one opening; they were wrapped with black vinyl tape except for a clear area on the top from which we could observe the mantis shrimp inside (see also Green & Patek, 2018; Green & Patek, 2015). The dimensions of mock burrows are presented in Table A2.

Animal Collection and Calculating Ideal Mock Burrow Size

We collected mantis shrimp from natural coral rubble burrows in seagrass beds on the Caribbean coast of Panama (MiAmbiente permit SE/A-52-17) following methods in Ahyong, Caldwell, and Erdmann (2017). We sexed and measured the body length and body mass (following methods in Green & Patek, 2015; Green & Patek, 2018; Green, McHenry, & Patek, 2019) of each individual on the day of collection. We randomly chose two individuals to be paired in a contest and randomly assigned one to be a "resident" and the other an "intruder" (Fig. 1a). To determine the "ideal mock burrow" for each individual, we used the regression of *N. bredini* body length against burrow volume established by Steger (1987) for natural burrows. For each individual, we defined the ideal mock burrow as the mock burrow (of 11 sizes, above) that minimized the absolute value of the difference between the body length of a mantis shrimp predicted best-fit for the burrow and the body length of the individual (Fig. 1b). That is, an individual's ideal mock burrow was the mock burrow it would be predicted to inhabit given Steger's (1987) findings.

Experimental Design

The evening before contest trials, we placed the randomly-chosen intruder inside the burrow choice arena, a clear plastic arena (11.4 cm height x 30.5 cm length x 20.3 cm width) with 2-3 cm of sand on the bottom and five mock burrows distributed evenly along the arena's length (haphazard placement of burrows with respect to position in the arena, Fig. 1c). These burrows were the ideal burrow, as well as the two burrows immediately smaller and larger than the ideal burrow, for the individual's size. Thirteen of 68 intruders (19.1%) were so small that we did not have burrows two sizes too small for them; in addition to the ideal burrow and the two larger burrows, we gave these intruders burrows one size too small or no small burrows. We left the intruder in the burrow choice arena overnight.

The same evening as the burrow choice experiment, we placed the randomly-assigned resident and one mock burrow inside a second clear plastic arena (as above) for the staged contest experiments (Fig. 1d). We termed this burrow and arena the contest burrow and contest arena. To encourage the resident to establish residency in the contest burrow, the contest burrow was randomly chosen from up to five options: the ideal burrow for the resident's size and the two burrows immediately smaller and larger than the ideal burrow. If the resident was too small to have two burrow options smaller than the ideal burrow (12/68 contests, 17.5%), we chose the contest burrow from the subset including one burrow size too small or no small burrows (similar to the burrow choice experiment). We allowed the resident to acclimate to the contest burrow overnight.

Data Collection

The following morning, in the burrow choice arena, we recorded which of the five burrows the intruder inhabited. We marked "N/A" if the intruder was not in a burrow (14/68 trials, 21.0%). In the contest arena, we placed a grey laminated divider roughly 7 cm from the front of the contest burrow and set up two GoPro Hero 3+ (San Mateo, CA, USA) cameras to film the arena (one top-down and one side view). We then removed the intruder from the burrow choice experiment and introduced it behind the grey laminated divider in the contest arena. After 10 minutes, we removed the divider and filmed the contest arena for 20 minutes or until three competitive interactions had occurred (from initial aggressive behaviour until one competitor's retreat, as defined below), whichever came first. We then separated competitors and placed each individual inside a small, plastic, perforated tube in a larger circulating seawater tank until the end of all staged contests. We released most individuals at the end of the experiment or transported them to Duke University (MiAmbeinte permit SEX/A-48-17) for future studies.

From the videos of staged contests, we recorded behavioural data that quantified aggressive motivation, contest costs, and contest success. We recorded data from only the first competitive interaction to reduce the effects of previous fighting experience (reviewed in Hsu, Earley, & Wolf, 2006). Interactions started when both individuals had clearly noticed each other (usually, one individual approached its competitor) and ended when one individual made a clear, directed retreat away from its competitor. We recorded: 1) the duration until the first aggressive behaviour (defined as a visual "meral spread" display, a lunge, or a strike with the raptorial appendage; see Dingle & Caldwell, 1969), 2) which individual made the first aggressive behaviour, 3) the number of strikes delivered by the resident and, separately, the intruder, 4) the duration of the contest (i.e., the time until one individual retreated), and 5) which individual won (either took or remained in the burrow when its competitor retreated). Metrics (1) and (2) quantified aggressive motivation—more motivated individuals should show aggressive behaviour more quickly and be more likely to be aggressive first. Metrics (3) and (4) are established metrics of contest costs in this system: contests with more strikes and longer durations are costlier than contests with fewer strikes and shorter durations (Green & Patek, 2018; Green et al., 2019). Metric (3) also functioned as a measure of aggressive motivation: more motivated individuals should deliver more strikes. Finally, metric (5) quantified contest success.

Statistical Analysis

All analyses were completed in R version 3.5.1 (R Core Team, 2018). All data used in this study and an R code for data analysis are in the Supplementary Material.

Burrow Choice Experiment

Because some individuals were too small to have the full complement of five burrow options, we first subset our burrow choice data into two datasets: one for the small individuals offered a subset of burrow options and another for individuals offered all five burrow options. For each dataset, we used a binomial test (binom.test function in R) to test whether the proportion of individuals that chose the ideal mock burrow was different than expected by chance. We also calculated the "chosen burrow match" for each dataset, defined as the body length of an individual best-fit for the chosen mock burrow minus the focal individual's body length.

Staged Contests

32 of the 68 staged contests (47%) did not involve aggressive behaviour (defined above) by either competitor. We removed these contests from our analysis (final contest *N* = 36). We used generalized linear models (GLMs) in the lme4 package in R (Bates, Maechler, Bolker, & Walker, 2015) to examine whether relative body mass (in grams; intruder – resident) and the match between intruder or, independently, resident body length and the body length of an

individual best-fit for the contest burrow (in millimetres; contest burrow best-fit body length – intruder or resident body length; hereafter "intruder burrow match" and "resident burrow match") predicted whether contests did or did not involve aggressive behaviour. The burrow match variables were fit with a second-order (quadratic) polynomial using the poly function in R. This allowed the probability of aggressive behaviour to be maximized at any burrow match value and decrease in either direction from this maximum. All predictor variables were centred, following recommendations by Schielzeth (2010). Due to sample size constraints, we could not run a model with all predictor variables and their interactions. Instead, we built separate models and used Wald tests to ask whether relative mass, intruder burrow match, or resident burrow match were significant predictors of whether a contest involved aggressive behaviour. Each model had a binomial error function.

For contests that did involve aggression, we first used a chi-squared test to examine whether residents were more likely to win than intruders. Then, we used generalized linear models (GLMs) in the lme4 package in R (Bates et al., 2015) to test how the intruder's ability to evict the resident was predicted by RHP (relative body mass) and resource value (burrow match, defined above) for intruders and residents. As above, because of sample size constraints we could not run a model with all predictor variables and their interactions. Instead, to test which predictor (relative mass, intruder burrow match, resident burrow match) best predicted intruder contest success, we built separate models and tested which model was best supported (see below). Each model had a binomial error function and all predictor variables were centred. The burrow match variables were fit with a quadratic polynomial, as above, which allowed the probability of intruder win to be maximized at any burrow match value and decrease in either direction from this maximum. We also tested models in which we used an absolute value metric of intruder (and, separately, resident) burrow match, defined as the absolute value of the difference between intruder (or resident) body length and the body length of an individual best-fit to the contest burrow. These models, similar to the approach taken by Hazlett (1978) for hermit crabs, make the *a priori* assumption that the probability of intruder win is maximized when intruder body length is equal to the best-fit body length of the contest burrow. These models also treat burrows both larger and smaller than ideal as equivalent. We calculated model fits using AICc scores (AIC corrected for small sample size; AICc function in MuMIn package in R; Barton, 2019) and then calculated model likelihoods and model weights following Burnham, Anderson, and Huyvaert (2010). The model with the lowest AICc score, resulting in highest likelihood and highest model weight, was the model that best predicted intruder contest success.

We also used GLMs to test how behavioural metrics of aggressive motivation and contest costs were influenced by RHP and resource value, as well as if winning and losing intruders differed in competitive strategies. We built 11 different models for each of four dependent variables. Dependent variables were: 1) total contest duration, 2) total number of contest strikes (sum of resident and intruder strikes), 3) duration until first aggressive behaviour, and 4) probability that the intruder gave the first aggressive behaviour. The duration variables were $\log_{10}$-transformed ($\log_{10}$[value + 1]) to improve normality. The duration models had a Gaussian error distribution, the number of strikes model had a Poisson error distribution, and the model predicting the probability the intruder gave the first aggressive behaviour had a binomial error distribution. The predictor variables fit in separate models for each dependent variable were 1) whether intruders won or lost (hereafter, “intruder win/loss”), 2) relative mass, 3) relative mass, intruder win/loss, and their interaction (hereafter, “relative mass x intruder win/loss”), 4) intruder burrow match, 5) intruder burrow match x intruder win/loss, 6) resident burrow match, and 7) resident burrow match x intruder win/loss. As above, burrow match variables were fit with a second-order polynomial and all predictor variables were centred. We also fit models with absolute value metrics for burrow match, and their interaction with intruder win/loss (Models 8-11 for each dependent variable). As in the contest outcome analyses, we compared model fits using AICc scores and model likelihoods and weights. Model AICc and ΔAICc values, as well as model likelihoods and model weights, are reported in Table A3. In the Results, we report the AICc of the best-fit model, the ΔAICc of the next best-fit model, and the model weight (w_i) of the best-fit model.

Ethical Note

This study adhered to all Panamanian and US guidelines for animal welfare in research (Panamanian MiAmbiente permits SE/A-52-17& SEX/A-48-17), as well as to the ABS guidelines for use of animals in research. We attempted to minimize disturbance and handling during animal collection, measurement, and experimentation. We also stopped any contest trial in which it appeared one individual was in imminent danger of long-term harm (e.g., death or significant injury).

RESULTS

Burrow Choice Experiment

Fourteen of 68 individuals (20.6%) did not choose any burrow during the overnight burrow choice experiment. Individuals that chose burrows did not choose the ideal mock burrows differently than predicted by chance. Both individuals too small to have all five burrow options (observed proportion = 0.33, expected proportion = 0.29, $P = 0.73$, mean ± sd chosen burrow match = 3.10 ± 2.49 mm) and individuals with the full complement of burrow options (observed proportion = 0.26, expected proportion = 0.20, $P = 0.26$, mean ± sd chosen burrow match = 2.32 ± 2.85 mm) chose burrows larger than expected.

Staged Contest Experiment

None of the relative body mass of the two competitors ($z_{66} = 0.043$, $P = 0.97$), intruder burrow match (first polynomial term $z_{65} = 0.28$, $P = 0.78$, second polynomial term $z_{65} = -0.44$, $P = 0.66$), or resident burrow match (first polynomial term $z_{65} = 1.50$, $P = 0.14$, second polynomial term $z_{65} = 0.15$, $P = 0.89$) predicted whether a contest involved aggression.

Contest Outcomes

Residents won 25 of 36 staged contests (69.4%; $\chi^2_1 = 4.69$, $P = 0.03$). The best-fit model predicting the probability of intruder win was the quadratic fit to intruder burrow match (Table A3, AICc = 32.73, ΔAICc of next model = 4.60, model weight $w_i = 0.91$). The probability an intruder won was maximized when it was 6.34 mm larger than the ideal size for the contest burrow; this probability decreased as intruder burrow match increased or decreased (Fig. 2a). Intruders only won contests in which they had greater body mass than residents and had a 50% chance of winning when their body mass was 0.49 g greater than residents (Fig. 2b, competitor body mass mean ± sd = 0.87 ± 0.46 g, min = 0.29 g, max = 2.31 g). The probability of intruder win was not strongly correlated with any of 1) the quadratic fit to resident burrow match (Fig. 2c), 2) the absolute value of intruder burrow match, or 3) the absolute value of resident burrow match (Table A3).

Contest Costs and Aggressive Behaviours

Total contest duration was equally well predicted by intruder win/loss, the quadratic fit to resident burrow match, and the absolute value of resident burrow match. However, model weights were low and plotting the relationship between contest duration and resident burrow match suggested a linear fit to the raw (not absolute) values of resident burrow match might be more appropriate. A *post-hoc* GLM using a linear fit to raw resident burrow match was a better fit for the data than any other model (AICc = 57.60, ΔAICc = 2.02, w_i = 0.37). This linear relationship showed that contests were shorter as residents were smaller than ideal for the contest burrow (Fig. 3a).

The total number of strikes during contests was best predicted by intruder win/loss (AICc = 84.91, ΔAICc = 3.34, w_i = 0.65). Contests in which intruders won involved more strikes (Fig. 3b; mean ± sd for intruder win = 1.27 ± 1.01, loss = 0.48 ± 0.96). *Post-hoc* GLMs showed that winning intruders delivered more strikes (estimate ± sd = 1.29 ± 0.57, Wald test z_{34} = 2.27, *P* = 0.02; mean ± sd for intruder win = 0.73 ± 0.65, loss = 0.20 ± 0.50), but did not receive more strikes from residents (estimate ± sd = 0.67 ± 0.56, Wald test z_{34} = 1.20, *P* = 0.23, mean ± sd for intruder win = 0.55 ± 0.69; loss = 0.28 ± 0.61).

The duration until the first aggressive behaviour was best predicted by intruder win/loss (AICc = 36.54, ΔAICc = 1.61, w_i = 0.33). The first aggressive behaviour occurred more quickly in contests in which the intruder won (Fig. 3c).

Finally, the best-fit model predicting the probability that the intruder gave the first aggressive behaviour included relative mass, intruder win/loss, and their interaction (AICc = 47.12, ΔAICc = 2.97, w_i = 0.67). Losing intruders were less likely to give the first aggressive behaviour as relative mass increased (i.e., as they became larger than residents). However, winning intruders were *more* likely to give the first aggressive behaviour as their relative mass increased (Fig. 3d).

DISCUSSION

Our results show quadratic assessment of resource value—here, the match between competitor size and burrow size—in mantis shrimp contests. Intruding mantis shrimp were most likely to win when contested burrows were slightly smaller than what we predicted was ideal for their body size. Intruder success decreased as burrow match increased or decreased from this value. Contest costs (contest duration, number of strikes) and behaviours indicating competitive motivation (number of strikes, duration to and likelihood of giving the first aggressive behaviour) were driven mostly by differences between intruders that won *versus* those that lost, although relative body mass and resident burrow matching were also important. Below, we interpret these results in the context of mantis shrimp ecology and behaviour, and we discuss the implications of quadratic resource value assessment to animal contests more broadly.

Burrow Choice

Mantis shrimp preferred mock burrows larger than predicted ideal for their body length. Our use of mock burrows—which was intended to standardize conditions for our experimental design—may have affected these results. We pre-built burrows with set lengths and diameters, while the natural burrows measured by Steger (1987) likely had more variable dimensions. Furthermore, our burrows were built from smooth-sided tubing, while natural burrows occur in rock and rubble. Mantis shrimp are adept modifiers of natural burrows, using appendage strikes to widen too-narrow burrows and using rock and sand to fill in too-large burrows (P.A.G., *personal observation*). While the individuals we tested could not widen mock burrows by striking, perhaps with more time in which to establish residency, individuals would have filled in larger mock burrows. Future work might use more nuanced variation in mock burrow dimensions to test burrow choice or might observe mantis shrimp behaviour inside larger mock burrows to ask if and how they modify burrow size.

Intruder Resource Value Assessment

Intruders were most likely to win contests when the contest burrow was slightly smaller than ideal (Fig. 2a), with the likelihood of success decreasing as burrow match increased or decreased from this value. Intruders that won were more aggressive than intruders that lost, delivering more strikes (Fig. 3b) and being more likely to show aggression first, especially as they increased in mass relative to residents (Fig. 3d).

One interpretation of the burrow choice and staged contest results is that, during contests, intruders use burrow size as a means of assessing both resource value (in a quadratic fashion) and resident RHP (body size). When given a choice of several unoccupied burrows (choice experiment), individuals chose burrows larger than the predicted ideal size. During contests, however, intruders must evict burrow residents that are often hidden inside the burrow, such that initial assessment of resident RHP might be difficult (Steger & Caldwell, 1983; Taylor & Patek, 2010). Intruders might overcome this lack of RHP information by taking advantage of the tight correlation between burrow volume and burrow resident size (Steger, 1987), assessing both resource value and resident RHP *via* burrow size. That is, intruders might assess a burrow that is slightly smaller than their ideal as containing a resident small enough to defeat. Such a burrow would also, if the intruder won, be a valuable resource while not being too small to defend in future contests. Our data on contest outcomes supports this hypothesis (Table A3). However, contest behaviours (e.g., number of strikes) were not well-explained by intruder burrow match, only intruder win/loss (Table A3). Future experiments—for example, relating mantis shrimp ability to perceive spatial detail (visual acuity; Caves, Brandley, & Johnsen, 2018) with natural variation in burrow entrance size—might show how intruders assess burrow value from outside the burrow.

While our model comparison results suggest that resource value was the strongest influence on contest outcomes (Table A3), sample size constraints precluded our ability to test the relative effects of resource value, resource ownership, and RHP. In our dataset, intruder burrow match and relative mass were strongly and negatively correlated (Pearson correlation = -0.85): larger intruders were more likely to be paired with smaller residents and to compete over smaller burrows. It is likely that resource value, RHP and resource ownership are each important to determining mantis shrimp contest outcomes (see also Green & Patek, 2018). Studies in other taxa, like jumping spiders (Kasumovic, Mason, Andrade, & Elias, 2010), have shown that assessment of resource ownership, resource value, and RHP all determine variation in contest outcomes and behaviours. Future work in mantis shrimp could further probe these connections by controlling for more variation in RHP and resource value relationships, such as by holding relative RHP constant while varying only burrow size.

Burrow Residents

In contrast to intruders, we found little evidence that residents assessed burrow size during contest experiments. While residents had a resource ownership advantage, they showed no directional change in their likelihood of contest success as the contest burrow changed in size relative to their body size (Fig. 2c, Table A3). Testing contest outcomes is not the only means of establishing resource value assessment, however. Measuring variation in the costs competitors are willing to endure before giving up can also be important (Arnott & Elwood, 2007). Contests were shorter in duration (one measure of contest costs, Arnott & Elwood, 2009) as burrows became larger than ideal for resident body length (Fig. 3a). However, these changes may not have been driven by resident assessment of burrow value *per se*. Since duration as a cost metric is driven by the giving-up decision of the loser (i.e., the loser ends the contest through its retreat; Arnott & Elwood, 2007), resident resource value assessment would be shown by an interaction between resident burrow match and resident contest success. That is, if residents assessed larger-than-ideal burrows as less valuable, we would expect a negative correlation between resident burrow match and contest duration *specifically* for contests in which residents lost. However, a *post-hoc* GLM predicting contest duration from a linear fit to resident burrow match, intruder win/loss, and their interaction was a worse fit to the data than the model with only a linear fit to resident burrow match (ΔAICc = 4.26). Furthermore, the interaction term in this model was not significant (estimate ± SE = -0.00 ± 0.06, t_{32} = -0.04, P = 0.97). Therefore, there is no evidence that losing residents gave up earlier when contest burrows were larger than ideal. To ensure the resident took up residency during contest experiments, we limited the sizes of contest burrow offered to the resident (see Methods). However, intruder size was not taken into account when choosing the contest burrow; therefore, intruders encountered a wider variation of burrow matches (compare x-axes in Fig. 2A and 2C). Future work might try to control for this difference in variation between resident and intruder burrow match.

Evidence that competitors with distinct roles (here, residents and intruders) show different resource value assessment strategies is not uncommon. Arnott and Elwood (2008) described several examples where resource owners assess resource value while intruders do not. For example, in contests over females, male orb web spiders that are already guarding a female adjust their contest behavior according to female fecundity, while intruding males appear unable to gather similar information (Hack, Thompson, & Fernandes, 1997). Our results are surprising in that it was not resource owners, but *intruders* that showed evidence of resource value assessment. We suggest that, for mantis shrimp, the importance of resource ownership outweighs that of resource value. Resident mantis shrimp might be able to assess burrow size. However, because a burrow is so important as a refuge from predators (Berzins & Caldwell, 1983) and as a place to mate and brood eggs (Caldwell, 1991, see also Introduction), residents may simply follow the rule that a burrow should be defended no matter its size.

Quadratic Resource Value Assessment

Our test of quadratic resource value assessment in mantis shrimp reveals dynamics that other approaches missed. For example, we also built statistical models using an absolute value metric of burrow match, which *a priori* fixed maximum resource value at the predicted ideal burrow size and treated larger- and smaller-than-ideal burrows as having equally-low resource value. This metric resulted in worse-fitting models predicting contest outcomes, costs, and behaviors (Table A3). These models may have had worse fits because the absolute value metric missed the fact that intruder success was higher for burrows that were smaller, but not larger, than ideal. This metric might also have missed the resulting interpretation that both resource value and RHP might be assessed *via* burrow size (see above).

Tests of quadratic resource value assessment in other species might further inform the fields of contest behaviour and resource ecology. For example, testing for quadratic resource value assessment in other species that inhabit shelters in a size-assortative manner (e.g., hermit crabs, Hazlett, 1978) might show whether resource value assessment influences size-assortative relationships in these species. Quadratic assessment may also occur over other contested resources, such as females (where fecundity rises then drops over the lifetime or seasonally e.g., Stokkebo & Hardy, 2000; Muschett, Umbers, & Herberstein, 2017) or food (if competitors adjust fighting behavior according to necessary energy intake, e.g., Ewald, 1985). In Table A1, we have noted experimental studies where quadratic resource value effects may occur but have not yet been explicitly tested.

Finally, theoretical models and experimental tests of resource value assessment might benefit from incorporating non-linear resource value relationships, just as non-linear relationships have recently informed the field of RHP assessment. A.V. Palaoro and Briffa (2017) showed how allometric growth patterns common among exaggerated animal weapons can lead to non-linear relationships between RHP and contest costs. They suggested that prior studies not accounting for this effect may have mischaracterized the role of weaponry in RHP assessment (A.V. Palaoro & Briffa, 2017). Similar non-linear relationships in resource value, such as quadratic resource value assessment, might inform models of resource value assessment while also explaining why some prior studies have found no evidence of resource value assessment (Arnott & Elwood, 2008).

ACKNOWLEDGEMENTS

We thank Dr. S.N. Patek for insights into experimental design and for providing research funding, Drs. G. Arnott and E.M. Caves for edits to the manuscript, two anonymous reviewers for helpful feedback, and the staff at the STRI Galeta Marine Laboratory for help carrying out the experiment. This study was supported by a National Science Foundation grant to Sheila Patek (NSF IOS #1439850). P.A. Green is currently supported by a Human Frontiers Science Program Fellowship (#LT000460/2019-L).

REFERENCES

Abrams, P. (1982). Intraspecific shell exchange in the hermit crab Clibanarius virescens (Krauss). *Journal of Experimental Marine Biology and Ecology*, *59*(1), 89-101.

Ahyong, S. T., Caldwell, R. L., & Erdmann, M. V. (2017). Collecting and processing stomatopods. *Journal of Crustacean Biology, 37*(1), 109-114. doi:10.1093/jcbiol/ruw005

Alcock, J., & Bailey, W. (1997). Success in territorial defence by male tarantula hawk wasps *Hemipepsis ustulata*: the role of residency. *Ecological Entomology, 22*(4), 377-383.

Arnott, G., & Elwood, R. W. (2007). Fighting for shells: how private information about resource value changes hermit crab pre-fight displays and escalated fight behaviour. *Proceedings of the Royal Society - B, 274*(1628), 3011-3017. doi:10.1098/rspb.2007.1196

Arnott, G., & Elwood, R. W. (2008). Information gathering and decision making about resource value in animal contests. *Animal Behaviour, 76*(3), 529-542. doi:10.1016/j.anbehav.2008.04.019

Arnott, G., & Elwood, R. W. (2009). Assessment of fighting ability in animal contests. *Animal Behaviour, 77*(5), 991-1004. doi:10.1016/j.anbehav.2009.02.010

Austad, S. N. (1983). A game theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*). *Animal Behaviour, 31*(1), 59-73.

Barreto, R. E., Carvalho, G. G. A., & Volpato, G. L. (2011). The aggressive behavior of Nile tilapia introduced into novel environments with variation in enrichment. *Zoology, 114*(1), 53-57.

Barton, K. (2019). MuMIn: Multi-model inference. R package version 1.43.6. Retrieved from https://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1-48. doi:10.18637/jss.v067.i01

Berzins, I. K., & Caldwell, R. L. (1983). The effect of injury on the agonistic behavior of the stomatopod, *Gonodactylus bredini* (Manning). *Marine Behavior and Physiology, 10*, 83-96.

Bridge, A. P., Elwood, R. W., & Dick, J. T. (2000). Imperfect assessment and limited information preclude optimal strategies in male–male fights in the orb-weaving spider *Metellina mengei*. *Proceedings of the Royal Society - B, 267*(1440), 273-279.

Briffa, M., & Elwood, R. (2001). Motivational change during shell fights in the hermit crab *Pagurus bernhardus*. *Animal Behaviour, 62*(3), 505-510.

Briffa, M., Hardy, I. C. W., Gammell, M. P., Jennings, D. J., Clarke, D. D., & Goubault, M. (2013). Analysis of animal contest data. In I. C. W. Hardy & M. Briffa (Eds.), *Animal Contests* (pp. 47-85): Cambridge University Press.

Brown, W. D., Chimenti, A. J., & Siebert, J. R. (2007). The payoff of fighting in house crickets: motivational asymmetry increases male aggression and mating success. *Ethology, 113*(5), 457-465.

Brown, W. D., Smith, A. T., Moskalik, B., & Gabriel, J. (2006). Aggressive contests in house crickets: size, motivation and the information content of aggressive songs. *Animal Behaviour, 72*(1), 225-233.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2010). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology, 65*(1), 23-35. doi:10.1007/s00265-010-1029-6

Caldwell, R. L. (1987). Assessment strategies in stomatopods. *Bulletin of Marine Science, 41*(2), 135-150.

Caldwell, R. L. (1991). Variation in reproductive behavior in stomatopod Crustacea. In R. Bauer & J. Martin (Eds.), *Crustacean Sexual Biology* (pp. 67-90). New York: Columbia University Press.

Caldwell, R. L., & Dingle, H. (1975). Ecology and evolution of agonistic behavior in stomatopods. *Naturwissenschaften, 62*, 214-222.

Campbell, L. D., Salazar, A. R., & Rypstra, A. L. (2020). Contests between web spiders: patience as a strategy for successful invasion. *Biological Invasions*, 1-16.

Caves, E. M., Brandley, N. C., & Johnsen, S. (2018). Visual acuity and the evolution of signals. *Trends in Ecology and Evolution, 33*(5), 358-372. doi:10.1016/j.tree.2018.03.001

Clutton-Brock, T., Albon, S. D., Gibson, R. M., & Guinness, F. E. (1979). The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Animal Behaviour, 27*, 211-225.

Cristol, D. A. (1992). Food deprivation influences dominance status in dark-eyed juncos, *Junco hyemalis*. *Animal Behaviour, 43*(1), 117-124.

Cross, F. R., & Jackson, R. R. (2011). Effects of prey–spider odour on intraspecific interactions of araneophagic jumping spiders. *Journal of Ethology, 29*(2), 321-327.

Crowley, P. H., Gillett, S., & Lawton, J. H. (1988). Contests between larval damselflies: empirical steps toward a better ESS model. *Animal Behaviour, 36*(5), 1496-1510.

Dale, S., & Slagsvold, T. (1995). Female contests for nest sites and mates in the pied flycatcher *Ficedula hypoleuca*. *Ethology, 99*(3), 209-222.

Dick, J. T., & Elwood, R. W. (1990). Symmetrical assessment of female quality by male *Gammarus pulex* (Amphipoda) during struggles over precopula females. *Animal Behaviour, 40*(5), 877-883.

Dingle, H., & Caldwell, R. L. (1969). The aggressive and territorial behaviour of the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). *Behaviour, 33*(1), 115-136.

Doake, S., & Elwood, R. W. (2011). How resource quality differentially affects motivation and ability to fight in hermit crabs. *Proceedings of the Royal Society - B, 278*(1705), 567-573. doi:10.1098/rspb.2010.1418

Dowds, B. M., & Elwood, R. W. (1983). Shell wars: assessment strategies and the timing of decisions in hermit crab shell fights. *Behaviour, 85*(1-2), 1-24.

Dowds, B. M., & Elwood, R. W. (1985). Shell wars II: the influence of relative size on decisions made during hermit crab shell fights. *Animal Behaviour, 33*(2), 649-656.

Elias, D. O., Botero, C. A., Andrade, M. C., Mason, A. C., & Kasumovic, M. M. (2010). High resource valuation fuels “desperado” fighting tactics in female jumping spiders. *Behavioral Ecology, 21*(4), 868-875.

Elwood, R., Wood, K., Gallagher, M., & Dick, J. (1998). Probing motivational state during agonistic encounters in animals. *Nature, 393*(6680), 66-68.

Elwood, R. W., & Briffa, M. (2001). Information gathering and communication during agonistic encounters: a case study of hermit crabs. *Advances in the Study of Behavior, 30,* 53-97.

Elwood, R. W., & Glass, C. W. (1981). Negotiation or aggression during shell fights of the hermit crab *Pagurus bernhardus? Animal Behaviour, 29*(4), 1239-1244.

Emlen, D. J. (2008). The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics, 39*(1), 387-413. doi:10.1146/annurev.ecolsys.39.110707.173502

Englund, G., & Olsson, T. I. (1990). Fighting and assessment in the net-spinning caddis larva *Arctopsyche ladogensis*: a test of the sequential assessment game. *Animal Behaviour, 39*(1), 55-62.

Englund, G., & Otto, C. (1991). Effects of ownership status, weight asymmetry, and case fit on the outcome of case contests in two populations of *Agrypnia pagetana* (Trichoptera: Phryganeidae) larvae. *Behavioral Ecology and Sociobiology, 29*(2), 113-120.

Ewald, P. W. (1985). Influence of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. *Animal Behaviour, 33*(3), 705-719.

Fernandez, E., Shi, X., & Li, Z. (2017). Ritualized fights among foraging cattle egrets following Père David's deer in Dafeng Nature Reserve. *Journal of Zoology, 302*(2), 73-78.

Figler, M. H., Blank, G. S., & Peeke, H. V. (1997). Maternal aggression and post-hatch care in red swamp crayfish, *Procambarus clarkii* (Girard): The influences of presence of offspring, fostering, and maternal molting. *Marine and Freshwater Behaviour and Physiology, 30*(3), 173-194.

Figler, M. H., Peeke, H. V., & Chang, E. S. (1997). Maternal aggression in American lobsters (*Homarus americanus* Milne-Edwards): shelter-related encounters against non-maternal female conspecifics. *Marine and Freshwater Behaviour and Physiology, 30*, 267-274.

Figler, M. H., Peeke, H. V., & Chang, E. S. (1998). Shelter-related aggression between adult male conspecific intruders and resident maternal American lobsters (*Homarus americanus*) with eggs at different stages of embryogenesis. *Marine and Freshwater Behaviour and Physiology, 31*(3), 151-166.

Flink, H., & Svensson, P. A. (2015). Nest size preferences and aggression in sand gobies (*Pomatoschistus minutus*). *Behavioral Ecology and Sociobiology, 69*(9), 1519-1525.

Gabor, C. R., & Jaeger, R. G. (1995). Resource quality affects the agonistic behaviour of territorial salamanders. *Animal Behaviour*, *49*(1), 71-79.

Gherardi, F. (1996). Effects of shell status and social context on the agonistic behavior of the tropical hermit crab, *Clibanarius signatus*. *Journal of Ethology, 14*(2), 111-121.

Gherardi, F. (2006). Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus*. *Behavioral Ecology and Sociobiology, 59*(4), 500-510.

Goubault, M., Cortesero, A. M., Poinsot, D., Wajnberg, E., & Boivin, G. (2007). Does host value influence female aggressiveness, contest outcome and fitness gain in parasitoids? *Ethology, 113*(4), 334-343.

Goubault, M., Scott, D., & Hardy, I. C. (2007). The importance of offspring value: maternal defence in parasitoid contests. *Animal Behaviour, 74*(3), 437-446.

Green, P. A., McHenry, M. J., & Patek, S. N. (2019). Context-dependent scaling of weapon kinematics and energetics in mantis shrimp (Stomatopoda). *Journal of Experimental Biology, 222*, 1-12.

Green, P. A., & Patek, S. N. (2015). Contests with deadly weapons: telson sparring in mantis shrimp (Stomatopoda). *Biology Letters, 11*, 1-4. doi:10.1098/rsbl.2015.0558

Green, P. A., & Patek, S. N. (2018). Mutual assessment during ritualized fighting in mantis shrimp (Stomatopoda). *Proceedings of the Royal Society - B, 285*(1871), 1-9. doi:10.1098/rspb.2017.2542

Gruber, C., Tulonen, J., Kortet, R., & Hirvonen, H. (2016). Resource availability and predation risk influence contest behavior and dominance hierarchies in crayfish. *Behavioral Ecology and Sociobiology, 70*(8), 1305-1317.

Hack, M. A., Thompson, D. J., & Fernandes, D. M. (1997). Fighting in males of the autumn spider, *Metellina segmentata*: effects of relative body size, prior residency and female value on contest outcome and duration. *Ethology, 103*(6), 488-498.

Hansen, A. J. (1986). Fighting behavior in bald eagles: a test of game theory. *Ecology, 67*(3), 787-797.

Hardy, I. C. W., & Briffa, M. (2013). *Animal Contests*. Cambridge, UK: Cambridge University Press.

Hazlett, B. A. (1978). Shell exchanges in hermit crabs: aggression, negotiation, or both? *Animal Behaviour*, *26*(4).

Hazlett, B. A. (1987). Information transfer during shell exchange in the hermit crab *Clibanarius antillensis*. *Animal Behaviour, 35*(1), 218-226.

Hazlett, B. A. (1989). Shell exchanges in the hermit crab *Calcinus tibicen*. *Animal Behaviour, 37*(1), 104-111.

Hazlett, B. A. (1996). Assessments during shell exchanges by the hermit crab *Clibanarius vittatus*: the complete negotiator. *Animal Behaviour*, *51*(3), 567-573.

Hoefler, C. D., Guhanarayan, G., Persons, M. H., & Rypstra, A. L. (2009). The interaction of female condition and mating status on male-male aggression in a wolf spider. *Ethology, 115*(4), 331-338.

Hollander, F. A., Titeux, N., & Van Dyck, H. (2012). Territorial resource valuation deviates from habitat quality in an ecologically trapped, long-distance migratory bird. *Behavioral Ecology and Sociobiology, 66*(5), 777-783.

Hsu, Y., Earley, R. L., & Wolf, L. L. (2006). Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. *Biological Reviews*, *81*(1), 33-74. doi:10.1017/S146479310500686X

Hughes, J., Harvey, I., & Hubbard, S. (1994). Host-searching behavior of *Venturia canescens* (Grav.) (Hymenoptera: Ichneumonidae): Interference—the effect of mature egg load and prior behavior. *Journal of Insect Behavior, 7*(4), 433-454.

Humphries, E. L., Hebblethwaite, A. J., Batchelor, T. P., & Hardy, I. C. (2006). The importance of valuing resources: host weight and contender age as determinants of parasitoid wasp contest outcomes. *Animal Behaviour*, *72*(4), 891-898.

Jakob, E. M. (1994). Contests over prey by group-living pholcids (*Holocnemus pluchei*). *Journal of Arachnology*, 39-45.

Jennings, D. J., Gammell, M. P., Carlin, C. o. M., & Hayden, T. J. (2004). Effect of body weight, antler length, resource value and experience on fight duration and intensity in fallow deer. *Animal Behaviour, 68*(1), 213-221. doi:10.1016/j.anbehav.2003.11.005

Johnsson, J. I., & Forser, A. (2002). Residence duration influences the outcome of territorial conflicts in brown trout (*Salmo trutta*). *Behavioral Ecology and Sociobiology, 51*(3), 282-286.

Judge, K. A., Ting, J. J., Schneider, J., & Fitzpatrick, M. J. (2010). A lover, not a fighter: mating causes male crickets to lose fights. *Behavioral Ecology and Sociobiology, 64*(12), 1971-1979.

Kasumovic, M. M., Mason, A. C., Andrade, M. C. B., & Elias, D. O. (2010). The relative importance of RHP and resource quality in contests with ownership asymmetries. *Behavioral Ecology, 22*(1), 39-45. doi:10.1093/beheco/arq161

Keeley, E. R., & Grant, J. W. (1993). Asymmetries in the expected value of food do not predict the outcome of contests between convict cichlids. *Animal Behaviour, 45*(5), 1035-1037.

Keil, P. L., & Watson, P. J. (2010). Assessment of self, opponent and resource during male–male contests in the sierra dome spider, *Neriene litigiosa*: Linyphiidae. *Animal Behaviour, 80*(5), 809-820.

Kilgour, R., Norris, D., & McAdam, A. (2020). Carry-over effects of resource competition and social environment on aggression. *Behavioral Ecology, 31*(1), 140-151.

Klar, N. M., & Crowley, P. H. (2012). Shelter availability, occupancy, and residency in size-asymmetric contests between rusty crayfish, *Orconectes rusticus*. *Ethology, 118*(2), 118-126.

Krebs, J. R. (1982). Territorial defence in the great tit (*Parus major*): do residents always win? *Behavioral Ecology and Sociobiology, 11*(3), 185-194.

Laidre, M. E., & Elwood, R. W. (2008). Motivation matters: cheliped extension displays in the hermit crab, *Pagurus bernhardus*, are honest signals of hunger. *Animal Behaviour, 75*(6), 2041-2047.

Lindström, K. (1988). Male-male competition for nest sites in the sand goby, *Pomatoschistus minutus*. *Oikos*, 67-73.

Lindström, K. (1992). The effect of resource holding potential, nest size and information about resource quality on the outcome of intruder-owner conflicts in the sand goby. *Behavioral Ecology and Sociobiology, 30*(1), 53-58.

Liu, P. C., & Hao, D. J. (2019). Effect of variation in objective resource value on extreme male combat in a quasi-gregarious species, *Anastatus disparis*. *BMC Ecology, 19*(1), 21. doi:10.1186/s12898-019-0237-9

Mathiron, A. G., Earley, R. L., & Goubault, M. (2019). Juvenile hormone manipulation affects female reproductive status and aggressiveness in a non-social parasitoid wasp. *General and Comparative Endocrinology, 274,* 80-86.

Mathiron, A. G. E., Pottier, P., & Goubault, M. (2018). Let the most motivated win: resource value components affect contest outcome in a parasitoid wasp. *Behavioral Ecology, 29*(5), 1088-1095. doi:10.1093/beheco/ary084

McCallum, E. S., Gulas, S. T., & Balshine, S. (2017). Accurate resource assessment requires experience in a territorial fish. *Animal Behaviour, 123*, 249-257.

Mohamad, R., Monge, J.-P., & Goubault, M. (2010). Can subjective resource value affect aggressiveness and contest outcome in parasitoid wasps? *Animal Behaviour*, *80*(4), 629-636.

Mohamad, R., Monge, J.-P., & Goubault, M. (2012). Wait or fight? Ownership asymmetry affects contest behaviors in a parasitoid wasp. *Behavioral Ecology, 23*(6), 1330-1337.

Mohamad, R., Monge, J. P., & Goubault, M. (2013). Do resource value and ownership status affect intensity and resolution of contests in a parasitoid wasp? *Entomologia Experimentalis et Applicata*, *147*(2), 99-109.

Montgomery, E. L., & Caldwell, R. L. (1984). Aggressive brood defense by females in the stomoatopod *Gonodactylus bredini*. *Behavioral Ecology and Sociobiology*, *14*(4), 247-251.

Muschett, G., Umbers, K. D., & Herberstein, M. E. (2017). Within-season variability of fighting behaviour in an Australian alpine grasshopper. *PLoS One, 12*(4), e0171697. doi:10.1371/journal.pone.0171697

Neat, F. C., Huntingford, F. A., & Beveridge, M. M. (1998). Fighting and assessment in male cichlid fish: the effects of asymmetries in gonadal state and body size. *Animal Behaviour, 55*(4), 883-891.

Nolen, Z. J., Allen, P. E., & Miller, C. W. (2017). Seasonal resource value and male size influence male aggressive interactions in the leaf footed cactus bug, *Narnia femorata*. *Behavioural Processes, 138*, 1-6.

Nosil, P. (2002). Food fights in house crickets, *Acheta domesticus*, and the effects of body size and hunger level. *Canadian Journal of Zoology, 80*(3), 409-417.

O'Connor, C. M., Reddon, A. R., Ligocki, I. Y., Hellmann, J. K., Garvy, K. A., Marsh-Rollo, S. E., . . . Balshine, S. (2015). Motivation but not body size influences territorial contest dynamics in a wild cichlid fish. *Animal Behaviour, 107,* 19-29.

Osborne, L., Umbers, K. D., & Keogh, J. S. (2013). The effects of perch height, time in residence and distance from opponent on aggressive display in male lizards. *Acta Ethologica, 16*(1), 41-46.

Palaoro, A. V., & Briffa, M. (2017). Weaponry and defenses in fighting animals: how allometry can alter predictions from contest theory. *Behavioral Ecology, 00*(00), 1-9. doi:10.1093/beheco/arw163

Palaoro, A. V., Velasque, M., Santos, S., & Briffa, M. (2017). How does environment influence fighting? The effects of tidal flow on resource value and fighting costs in sea anemones. *Biology Letters, 13*(5), 20170011.

Parker, G. A. (1974). Assessment strategy and the evolution of fighting behavior. *Journal of Theoretical Biology, 47*, 223-243.

Peeke, H. V., Twum, M., Finkelstein, J. E., & Figler, M. H. (1995). Maternal aggression in red swamp crayfish (*Procambarus clarkii*, Girard): the relation between reproductive status and outcome of aggressive encounters with male and female conspecifics. *Behaviour, 132*(1-2), 107-125.

Percival, D., & Moore, P. (2010). Shelter size influences self-assessment of size in crayfish, *Orconectes rusticus*: Consequences for agonistic fights. *Behaviour, 147*(1), 103-119. doi:10.1163/000579509x12512685881053

Petersen, A., Nielsen, K. T., Christensen, C. B., & Toft, S. (2010). The advantage of starving: success in cannibalistic encounters among wolf spiders. *Behavioral Ecology, 21*(5), 1112-1117.

Popp, J. W. (1987). Resource value and dominance among American goldfinches. *Bird Behavior, 7*(2), 73-77.

R Core Team. (2018). R: A language and environment for statistical computing (Version 3.0.1). Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org

Reaka, M. L. (1980). On learning and living in holes by mantis shrimp. *Animal Behaviour, 28*(111-115).

Riechert, S. E. (1979). Games spiders play: II. Resource assessment strategies. *Behavioral Ecology and Sociobiology*, 121-128.

Riechert, S. E. (1984). Games spiders play. III: cues underlying context-associated changes in agonistic behaviour. *Animal Behaviour, 32*(1), 1-15.

Riechert, S. E. (1988). The energetic costs of fighting. *American Zoologist, 28*, 877-884.

Riechert, S. E. (1998). Game theory and animal contests. In L. A. Dugatkin & H. K. Reeve (Eds.), *Game Theory and Animal Behavior* (pp. 64-93). New York, NY: Oxford University Press.

Rodriguez-Girones, M. A., Drummond, H., & Kacelnik, A. (1996). Effect of food deprivation on dominance status in blue-footed booby (*Sula nebouxii*) broods. *Behavioral Ecology, 7*(1), 82-88.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution, 1*(2), 103-113. doi:10.1111/j.2041-210X.2010.00012.x

Searcy, W. A., & Beecher, M. D. (2009). Song as an aggressive signal in songbirds. *Animal Behaviour, 78*(6), 1281-1292. doi:10.1016/j.anbehav.2009.08.011

Sigurjonsdottir, H., & Parker, G. (1981). Dung fly struggles: evidence for assessment strategy. *Behavioral Ecology and Sociobiology, 8*(3), 219-230.

Steger, R. (1987). Effects of refuges and recruitment on gonodactylid stomatopods, a guild of mobile prey. *Ecology, 68*(5), 1520-1533.

Steger, R., & Caldwell, R. L. (1983). Intraspecific deception by bluffing: a defense strategy of newly molted stomatopods (Arthropoda: Crustacea). *Science*, *221*(4610), 558-560.

Stockermans, B. C., & Hardy, I. C. (2013). Subjective and objective components of resource value additively increase aggression in parasitoid contests. *Biology Letters, 9*(4), 20130391.

Stokkebo, S., & Hardy, I. C. (2000). The importance of being gravid: egg load and contest outcome in a parasitoid wasp. *Animal Behaviour*, *59*(6), 1111-1118. doi:10.1006/anbe.2000.1407

Suzuki, Y., Yasuda, C., Takeshita, F., & Wada, S. (2012). Male mate choice and male–male competition in the hermit crab *Pagurus nigrofascia*: importance of female quality. *Marine Biology, 159*(9), 1991-1996.

Swierk, L., & Langkilde, T. (2013). Sizing-up the competition: factors modulating male display behavior during mate competition. *Ethology, 119*(11), 948-959.

Takeuchi, T., & Honda, K. (2009). Early comers become owners: effect of residency experience on territorial contest dynamics in a lycaenid butterfly. *Ethology, 115*(8), 767-773.

Taylor, J. R., & Patek, S. N. (2010). Ritualized fighting and biological armor: the impact mechanics of the mantis shrimp's telson. *Journal of Experimental Biology, 213*(20), 3496-3504.

Thornhill, R. (1984). Fighting and assessment in *Harpobittacus* scorpionflies. *Evolution,* 204-214.

Tibbetts, E. A., & Shorter, J. R. (2009). How do fighting ability and nest value influence usurpation contests in *Polistes* wasps? *Behavioral Ecology and Sociobiology, 63*(9), 1377-1385.

Torrezani, C. S., Pinho-Neto, C. F., Miyai, C. A., Sanches, F. H. C., & Barreto, R. E. (2013). Structural enrichment reduces aggression in *Tilapia rendalli*. *Marine and Freshwater Behaviour and Physiology, 46*(3), 183-190.

Verrell, P. A. (1986). Wrestling in the red-spotted newt (*Notophthalmus viridescens*): resource value and contestant asymmetry determine contest duration and outcome. *Animal Behaviour, 34*(2), 398-402.

Vieira, M. C., & Peixoto, P. E. C. (2013). Winners and losers: a meta-analysis of functional determinants of fighting ability in arthropod contests. *Functional Ecology*, *27*(2), 305-313. doi:10.1111/1365-2435.12051

Weiss, S. L., & Dubin, M. (2018). Male mate choice as differential investment in contest competition is affected by female ornament expression. *Current Zoology, 64*(3), 335-344.

Wyckhuys, K. A., Lopez Acosta, F., Garcia, J., & Jimenez, J. (2011). Host exploitation and contest behavior in a generalist parasitoid partially reflect quality of distinct host species. *Biocontrol Science and Technology, 21*(8), 953-968.

Yack, J. E., Gill, S., Drummond-Main, C., & Sherratt, T. N. (2014). Residency duration and shelter quality influence vibratory signalling displays in a territorial caterpillar. *Ethology*, *120*(4), 354-364.

Yasuda, C. I., Kaida, T., & Koga, T. (2020). Does prior residency interact with loss? A study of male–male contests in the hermit crab *Pagurus minutus*. *Ethology*.

Appendix Tables

Table A1. A survey of the type of tests of resource value assessment.

Species	**Common name**	**Resource**	**Type**	**Reference**
Anastatus disparis	Parasitoid wasp	Female mating status	C	Liu & Hao, 2019)
Dinarmus basali	Parasitoid wasp	Host abundance, time at host	C, LI	Mohamad, Monge, & Goubault, 2013
Eupelmus vuilleti	Parasitoid wasp	Habitat quality, host size	C, LI	Mohamad, Monge, & Goubault, 2010
Eupelmus vuilleti	Parasitoid wasp	Host type, egg load	C, LI	A. G. E. Mathiron et al., 2018
Eupelmus vuilleti	Parasitoid wasp	Host contact time	C	Mohamad, Monge, & Goubault, 2012
Goniozus legneri	Parasitoid wasp	Host size	C	Stockermans & Hardy, 2013
Goniozus nephantidis	Parasitoid wasp	Brood development	C	Goubault, Scott, & Hardy, 2007
Goniozus nephantidis	Parasitoid wasp	Host size	LI	Humphries, Hebblethwaite, Batchelor, & Hardy, 2006
Goniozus nephantidis	Parasitoid wasp	Female fecundity	LI*	Stokkebo & Hardy, 2000
Pachycrepoideus vindemmiae	Parasitoid wasp	Various (host & parasite)	C	Goubault, Cortesero, Poinsot, Wajnberg, & Boivin, 2007
Pachycrepoideus vindemmiae	Parasitoid wasp	Host species	C	Wyckhuys, Lopez Acosta, Garcia, & Jimenez, 2011
Pardosa prativaga	Parasitoid wasp	Female fecundity	LI	A. G. Mathiron, Earley, & Goubault, 2019
Venturia canescens	Parasitoid wasp	Fecundity, time probing host	LI*	Hughes, Harvey, & Hubbard, 1994
Calcinus tibicen	Hermit crab	Shell size	LI*	Hazlett, 1989
Clibanarius antillensis	Hermit crab	Shell size	C	Hazlett, 1987

Clibanarius signatus	Hermit crab	Shell size, damage	C	Gherardi, 1996
Clibanarius virescens	Hermit crab	Shell size	C	Abrams, 1982
Clibanarius vittatus	Hermit crab	Shell size	LI*	Hazlett, 1996
Pagurus bernhardus	Hermit crab	Food deprivation	LI	Laidre & Elwood, 2008
Pagurus bernhardus	Hermit crab	Shell interior	C	Arnott & Elwood, 2007
Pagurus bernhardus	Hermit crab	Shell species	C	Dowds & Elwood, 1983; R. Elwood, Wood, Gallagher, & Dick, 1998
Pagurus bernhardus	Hermit crab	Shell size	C, LI*	Dowds & Elwood, 1985; R.W. Elwood & Glass, 1981; R. Elwood et al., 1998; Briffa & Elwood, 2001; Hazlett, 1978; Doake & Elwood, 2011
Pagurus longicarpus	Hermit crab	Shell size	C	Gherardi, 2006
Pagurus minutus	Hermit crab	Female size	LI	Yasuda, Kaida, & Koga, 2020
Pagurus nigrofascia	Hermit crab	Female size, moult status	LI	Suzuki, Yasuda, Takeshita, & Wada, 2012
Agelenopsis aperta	Funnel-web spider	Web quality	LI, C	Riechert, 1979, 1984
Frontinella pyramitela	Bowl and doily spider	Female fecundity	LI	Austad, 1983
Holocnemus pluchei	Group-living spider	Prey size	LI	Jakob, 1994
Metellina mengei	Orb-weaving spider	Female size	LI	Bridge, Elwood, & Dick, 2000

Metellina segmentata	Autumn spider	Female size	C	Hack et al., 1997
Neriene litigiosa	Sierra dome spider	Female mating status	C	Keil & Watson, 2010
Pardosa milvina	Wolf spider	Female condition	C	Hoefler, Guhanarayan, Persons, & Rypstra, 2009
Pardosa prativaga	Wolf spider	Hunger level	C	Petersen, Nielsen, Christensen, & Toft, 2010
Phidippus clarus	Jumping spider	Moult status	LI	Elias, Botero, Andrade, Mason, & Kasumovic, 2010
Phidippus clarus	Jumping spider	Female size	LI	Kasumovic et al., 2010
Pholcus manueli and *Pholcus phalangioides*	Cellar spider	Hunger levels	C	Campbell, Salazar, & Rypstra, 2020
Portia fimbriata	Jumping spider	Food	C	Cross & Jackson, 2011
Astacus astacus	Noble crayfish	Food	C	Gruber, Tulonen, Kortet, & Hirvonen, 2016
Orconectes rusticus	Crayfish	Shelter size	C*	Percival & Moore, 2010
Orconectes rusticus	Rusty crayfish	Territory availability	C	Klar & Crowley, 2012
Procambarus clarkia	Red swamp crayfish	Territory residency, egg presence	C	Peeke, Twum, Finkelstein, & Figler, 1995; Figler, Blank, & Peeke, 1997
Cichlasoma nigrofasciatum	Convict cichlid	Food amount	LI	Keeley & Grant, 1993
Neolamprologus pulcher	Cichlid	Territory time, # of females	C	O'Connor et al., 2015
Tilapia zillii	Cichlid	Territory	LI	Neat, Huntingford, & Beveridge, 1998

Acheta domesticus	House cricket	Female presence	C	Brown, Smith, Moskalik, & Gabriel, 2006; Brown, Chimenti, & Siebert, 2007
Acheta domesticus	House cricket	Food availability	LI	Nosil, 2002
Gryllus pennsylvanicus	Fall field cricket	Female mating status, contact time	C	Judge, Ting, Schneider, & Fitzpatrick, 2010
Ctenophorus decresii	Agamid lizard	Territory (multiple aspects)	C	Osborne, Umbers, & Keogh, 2013
Sceloporus undulatus	Eastern fence lizard	Female quality	LI	Swierk & Langkilde, 2013
Sceloporus virgatus	Striped plateau lizard	Female size, reproductive state	LI	Weiss & Dubin, 2018
Arctopsyche ladogensis	Caddis larva	Food	C	Englund & Olsson, 1990
Arctopsyche ladogensis	Caddis larva	Larvae case size	C	Englund & Otto, 1991
Oreochromis niloticus	Nile tilapia	Territory quality	C	Barreto, Carvalho, & Volpato, 2011
Tilapia rendalli	Redbreast tilapia	Food	C	Torrezani, Pinho-Neto, Miyai, Sanches, & Barreto, 2013
Neogobius melanostomus	Round goby	Territory type	C	McCallum, Gulas, & Balshine, 2017
Pomatoschistus minutus	Sand goby	Nest size	C	Lindström, 1988, 1992; Flink & Svensson, 2015
Actinia equina	Sea anemone	Tidal flow	C	Palaoro, Velasque, Santos, & Briffa, 2017
Archilochus alexandri	Black-chinned hummingbird	Food	C*	Ewald, 1985

Carduelis tristis	American goldfinch	Food availability	LI	Popp, 1987
Chrysozephyrus smaragdinus	Butterfly	Territory residence time	C	Takeuchi & Honda, 2009
Dama dama	Fallow deer	Receptive females	LI	Jennings, Gammell, Carlin, & Hayden, 2004
Drepana arcuata	Masked birch caterpillar	Duration on territory	LI	Yack, Gill, Drummond-Main, & Sherratt, 2014
Drosophila melanogaster	Fruit fly	Food availability	C	Kilgour, Norris, & McAdam, 2020
Elaphurus davidianus	Pére David's deer	Food availability	LI	Fernandez, Shi, & Li, 2017
Ficedula hypoleuca	Pied flycatcher	Residence time	LI	Dale & Slagsvold, 1995
Gammarus pulex	Amphipod	Female size, time to moult	LI	Dick & Elwood, 1990
Haliaeetus leucocephalus	Bald eagle	Food availability	C	Hansen, 1986
Harpobittacus nigriceps	Scorpionfly	Nuptial prey size	LI	Thornhill, 1984
Hemipepsis ustulala	Tarantula hawk wasp	Residency time	LI	Alcock & Bailey, 1997
Homarus americanus	American lobster	Egg presence & development	C	Figler, Peeke, & Chang, 1997
Homarus americanus	American lobster	Territory residency	C	Figler, Peeke, & Chang, 1998
Junco hyemalis	Dark-eyed junco	Food deprivation	C	Cristol, 1992
Ischnura elegans	Damselfly larva	Food deprivation	C	Crowley, Gillett, & Lawton, 1988
Kosicuscola tristis	Alpine grasshopper	Seasonality	C*	Muschett et al., 2017
Lanius collurio	Red-backed shrike	Territory duration	LD	Hollander, Titeux, & Van Dyck, 2012
Narnia femorata	Leaf-footed cactus bug	Food quality	C	Nolen, Allen, & Miller, 2017
Notophthalmus viridescens	Red-spotted newt	Female size	LI	Verrell, 1986
Plethodon cinereus	Red-backed salamander	Food	C	Gabor & Jaeger, 1995

Polistes dominulus	Social paper wasp	Nest size	LI	Tibbetts & Shorter, 2009
Salmo trutta	Brown trout	Residence time	LI	Johnsson & Forser, 2002
Scatophaga stercoraria	Dung fly	Female fecundity	LI	Sigurjonsdottir & Parker, 1981
Sula nebouxii	Blue-footed booby	Food availability	LI	Rodriguez-Girones, Drummond, & Kacelnik, 1996

We searched the abstracts of literature cited by Arnott and Elwood (2008) and that has cited Arnott and Elwood (2008) as of April 2020 for evidence of a resource value test. We extracted the type of resource value assessment from the predictions and/or results as described in the abstract or, if needed, the main text. In the "Type" column, C = categorical (e.g., presence/absence, low/medium/high), LI = linearly increasing, LD = linearly decreasing. Asterisks in "Type" column reflect relationships that could be quadratic, but were not tested as such. For example, if absolute values were used to linearize an otherwise-quadratic relationship or if variation was categorized but could have shown a quadratic effect if studied along a continuum. Studies are organized first by number of different resources tested per taxonomic group (most to least), then alphabetically by genus.

Table A2. Dimensions of mock burrows and the length of *N. bredini* predicted by Steger (1987) to be best-fit for each mock burrow.

Burrow number	Burrow diameter (mm)	Burrow length (mm)	Burrow volume (mm^3)	Predicted *N. bredini* length (mm)
0	10.00	32.50	25.53	26.45
1	10.00	40.00	31.42	28.73
2	10.00	50.00	39.27	31.18
3	12.50	40.00	49.09	33.63
4	12.50	50.00	61.36	36.09
5	15.88	40.00	79.17	38.89
6	15.88	50.00	98.97	41.34
7	19.05	50.00	142.51	45.35
8	19.05	65.00	185.26	48.23
9	25.40	55.00	278.69	52.72
10	25.40	70.00	354.69	55.37

Table A3. Summary of model comparisons.

Response variable	Predictor(s)	AICc	ΔAICc	l_i	w_i
	Intruder burrow match	32.73	0.00	1.00	0.91

Probability of intruder win	Relative mass	37.32	4.60	0.10	0.09
	Intruder burrow match (absolute value)	44.52	11.79	0.00	0.00
	Resident burrow match (absolute value)	48.62	15.90	0.00	0.00
	Resident burrow match	51.02	18.30	0.00	0.00
Log_{10}(Total contest duration + 1)	Resident burrow match (linear fit)	57.60	0.00	1.00	0.37
	Intruder win/loss	59.62	2.02	0.36	0.14
	Resident burrow match	59.85	2.25	0.32	0.12
	Intruder burrow match (absolute value)	59.86	2.26	0.32	0.12
	Resident burrow match (absolute value)	60.84	3.24	0.20	0.07
	Relative mass	60.85	3.25	0.20	0.07
	Intruder burrow match (absolute value) x intruder win/loss	61.66	4.06	0.13	0.05
	Intruder burrow match	62.46	4.86	0.09	0.03
	Relative mass x intruder win/loss	64.55	6.95	0.03	0.01
	Resident burrow match (absolute value) x intruder win/loss	64.79	7.19	0.03	0.01
	Resident burrow match x intruder win/loss	67.56	9.96	0.01	0.00
	Intruder burrow match x intruder win/loss	68.33	10.73	0.00	0.00
Total number of strikes	Intruder win/loss	84.91	0.00	1.00	0.65
	Resident burrow match (absolute value) x intruder win/loss	88.25	3.34	0.19	0.12
	Relative mass x intruder win/loss	88.89	3.98	0.14	0.09
	Intruder burrow match (absolute value) x intruder win/loss	89.78	4.87	0.09	0.06
	Relative mass	91.39	6.48	0.04	0.03
	Resident burrow match x intruder win/loss	91.58	6.67	0.04	0.02
	Resident burrow match (absolute value)	93.21	8.30	0.02	0.01
	Intruder burrow match x intruder win/loss	93.29	8.38	0.02	0.01
	Intruder burrow match (absolute value)	93.69	8.78	0.01	0.01
	Resident burrow match	94.02	9.11	0.01	0.01
	Intruder burrow match	95.80	10.89	0.00	0.00
Log_{10}(Duration until first aggressive behaviour + 1)	Intruder win/loss	36.54	0.00	1.00	0.33
	Resident burrow match (absolute value)	38.15	1.61	0.45	0.15
	Resident burrow match	38.62	2.08	0.35	0.12
	Intruder burrow match (absolute value)	38.65	2.11	0.35	0.11
	Relative mass	38.89	2.35	0.31	0.10
	Resident burrow match (absolute value) x intruder win/loss	38.89	2.35	0.31	0.10

	Intruder burrow match (absolute value) x intruder win/loss	41.23	4.69	0.10	0.03
	Intruder burrow match	41.50	4.96	0.08	0.03
	Relative mass x intruder win/loss	41.65	5.11	0.08	0.03
	Resident burrow match x intruder win/loss	43.90	7.36	0.03	0.01
	Intruder burrow match x intruder win/loss	47.50	10.96	0.00	0.00
Probability that intruder gave first aggressive behaviour	Relative mass x intruder win/loss	47.12	0.00	1.00	0.67
	Intruder win/loss	50.09	2.97	0.23	0.15
	Intruder burrow match (absolute value) x intruder win/loss	53.02	5.90	0.05	0.04
	Relative mass	53.36	6.24	0.04	0.03
	Intruder burrow match (absolute value)	53.72	6.60	0.04	0.02
	Resident burrow match (absolute value)	53.74	6.62	0.04	0.02
	Intruder burrow match x intruder win/loss	54.24	7.12	0.03	0.02
	Resident burrow match (absolute value) x intruder win/loss	54.46	7.34	0.03	0.02
	Resident burrow match	55.25	8.13	0.02	0.01
	Intruder burrow match	55.79	8.67	0.01	0.01
	Resident burrow match x intruder win/loss	58.57	11.45	0.00	0.00

ΔAICc is relative to the best fit model, l_i is model likelihood, w_i is model weight. Models for each response variable are ranked by AICc score (lowest to highest).

FIGURE LEGENDS

Figure 1. A schematic of the experimental process. a) We collected and measured individuals, then randomly assigned one as an intruder (blue dot) and the other as a resident (orange dot). b) Using Steger's (1987) regression (solid line), we found the ideal mock burrow (from 11 burrow options, indicated by numbers along x-axis) for each individual, as well as a range of two smaller and two larger burrows. Burrows are black cylinders with white areas that indicate clear areas

from which we could observe behaviours inside. In (c) the burrow choice experiment, we (c1) allowed the intruder to choose among the range of 5 burrows, including (I) the ideal burrow, (S1, S2) the two burrows smaller than the ideal, and (L1, L2), the two burrows larger than the ideal. In (d) the staged contest experiment, we (d1) randomly chose one of the five burrow options for the resident (here, the burrow immediately smaller than ideal, S1) and allowed the resident to establish residency inside. The next day, we (c2) recorded the burrow choice of the intruder and (d2) confirmed the resident had established residency in the contest burrow. Finally, we (d3) moved the intruder into the contest arena and ran the contest trial.

Figure 2: The probability that an intruder won a contest as predicted by (a) the quadratic fit to intruder burrow match, (b), relative mass, and (c) the quadratic fit to resident burrow match. In each plot: fitted line represents fit of GLM as described in main text, grey region represents standard error, and solid vertical line indicates x-axis value of 0. In (a), dotted vertical line indicates the peak of the quadratic fit. In (b), dotted vertical line shows relative mass value where probability of intruder win = 0.50.

Figure 3. Contest costs and aggressive behaviours, including (a) total contest duration, (b) total number of contest strikes, (c) duration until the first aggressive behaviour, and (d) likelihood the intruder gave the first aggressive behaviour. In (a), solid line represents a linear fit and grey shaded region shows standard error. In (a) and (c), y-axis is $\log_{10}$-transformed. In (b) and (c), violin plot outlines depict kernel density estimations of the data, with boxplots superimposed inside. Box plots show the median (thick horizontal bar), interquartile range (box edges), and 1.5 x interquartile range (whiskers). Individual points are superimposed in violin plots; their position is randomly jittered to enhance clarity. In (d), circles and the solid line represent data from

contests in which the intruder lost; triangles and dashed line contests in which the intruder won. Lines show binomial GLM fits; shaded areas show standard errors.

FIGURES

Figure 1.

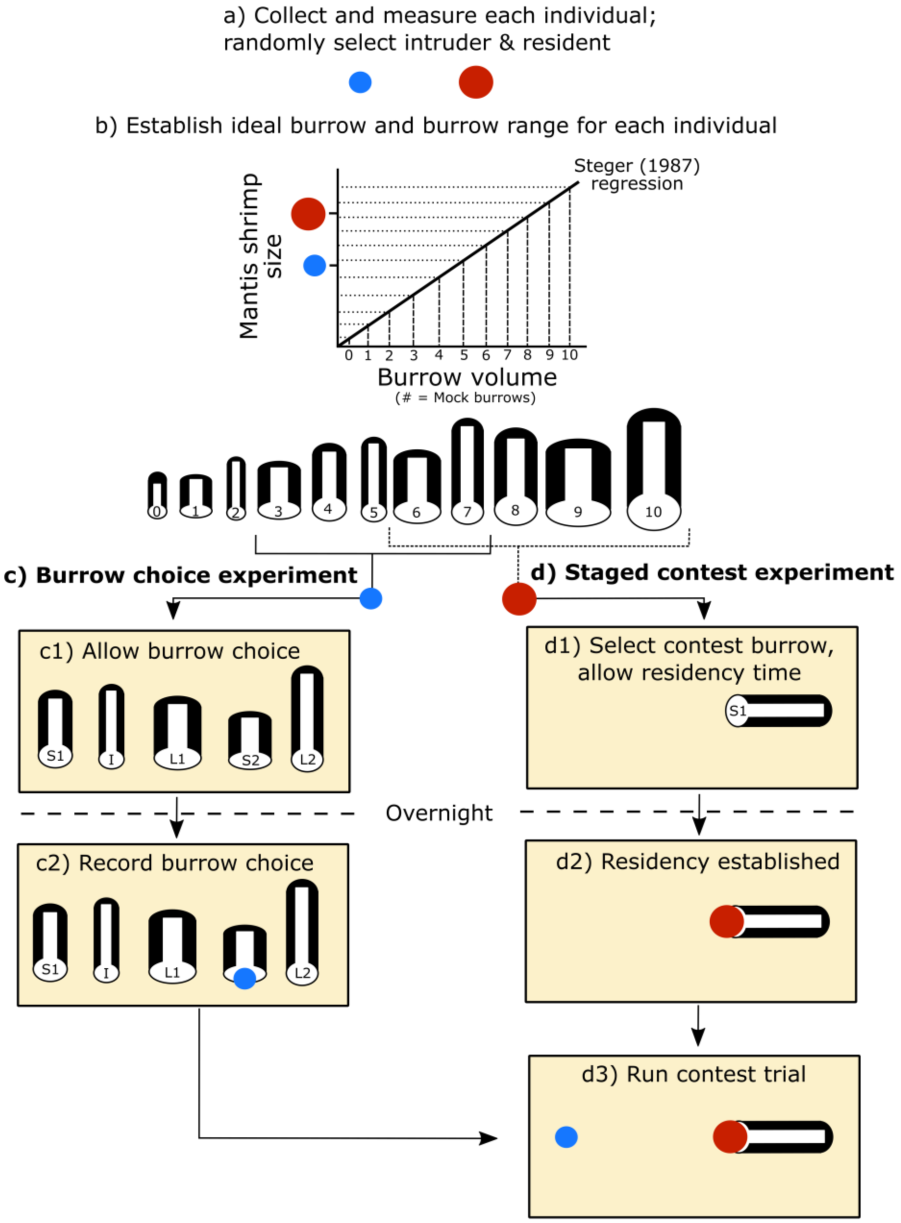

Figure 2.

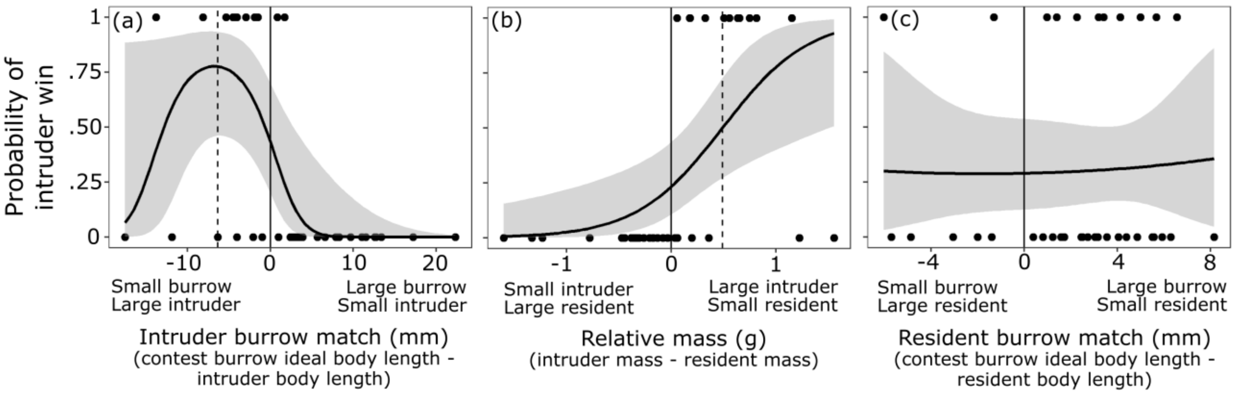

Figure 3.