

first contest. Experienced males were maintained in identical conditions to naive males until 3 days before their first contest. At this time, experienced males were placed in a clear plastic container ($17 \times 12 \times 6$ cm) with 0.5 cm of soil and 2 stock males (1 old and 1 young). These 2 males were randomly chosen from our stock population. This experimental setup allowed males to obtain information about their relative size and status within the population (i.e., small males would on average be smaller than the other males, large males would on average be large than the other males, and average-sized males would be on average intermediate between the other males) but did not allow males to gain direct experience of contest behavior, as social interactions between male burying beetles only escalate in the presence of a breeding resource (Pukoswki 1933). Focal males were left in these containers for approximately 24 h (preliminary observations were made to ensure that focal males interacted with stock males during this period) and then kept in isolation for 48 h prior to their first contest.

Prior to the establishment of our social experience treatment, we measured body size of all focal males. Pronotum width (to 0.1 mm) was measured 3 times using digital calipers, and the average of these recordings was used to calculate relative pronotum width (i.e., [focal male – nonfocal male]/focal male), a measure that gives the difference in size between focal and nonfocal individuals relative to the focal individuals absolute size. Including this measure as a covariate in all analyses allowed us to control for natural variation in intrinsic fighting ability, as relative pronotum width is known to be an important predictor of contest outcome in burying beetles (Safryn and Scott 2000). Including relative size in our analyses also allowed us to test whether male age or social experience mediated the relationship between male relative size and contest outcome. Analyses conducted using the size difference between males (i.e., focal male – nonfocal male) gave similar results, and so we only present results from analyses using relative pronotum width. After size measurements were taken, focal males were given a permanent mark on the right elytron to facilitate identification during social experience and contests. Previous studies in our laboratory using marked beetles have shown that this does not affect behavior (Hopwood et al 2013), and so for logistical reasons, we only marked focal beetles and not their opponents. This method of marking is unlikely to bias our results because focal males from all treatments were marked in the same way.

Experimental contests

Each focal male engaged in 2 experimental contests on consecutive days. This allowed us to investigate the effects of male age and social experience on contest behavior and contest outcome (analysis of the first contest), as well as how these treatments influenced winner and loser effects (analysis of second contest). For each contest, focal males were paired with opponents chosen at random from the nonfocal population. This method of pairing is preferred over size matching because it ensures randomization of variation in intrinsic fighting ability (Hsu et al. 2006), and it is more relevant to conditions beetles are likely to experience in the wild. All nonfocal males had been used in establishing our social experience treatment and so had a similar level of experience as our experienced focal males. We kept track of all individual identifications throughout the experiment to ensure that no focal male was paired with a sibling or an opponent that had been met previously, either during experimental contests or social experience treatment. Otherwise nonfocal males were allocated to contests randomly.

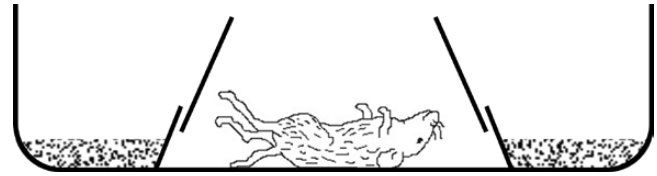


Figure 1

Arena for experimental contests. Escape holes remained covered until after the first interaction.

The contest arena (Figure 1) consisted of a clear perspex container ($17 \times 12 \times 6$ cm) with an inner ring made from an upturned flowerpot with the base cut off (diameter: 7 cm). The inner ring surrounded a small mouse carcass (19–30 g, sourced from Livefoods) and was designed to promote interactions between males, but had 2 openings that allowed males to escape into the outside area if necessary. Approximately 0.5 cm of soil was added to the outside area to allow individuals to burrow, and the inner ring was kept clear, in order to facilitate observation of agonistic interactions occurring on or near the carcass.

We recorded the mass of each mouse carcass (to 0.001 g, Ohaus Explorer balance) to control for any effects resource value may have on contest behavior or outcome (Fawcett and Johnstone 2010). There were no effects of carcass weight on any of our response variables (all $P > 0.473$), and so it was not considered further. A fresh carcass was used for each contest.

Behavioral observations

Both males were placed onto the carcass at the same time to avoid any effects of ownership on contest behavior or outcome as previous studies have shown that resource holders are more likely to win contests in *N. vespilloides* (Otronen 1988). Before introducing the males, the openings at the edge of the inner ring were covered to encourage pairs to interact. After initial contact, the cover was removed to allow individuals to escape into the outside area if necessary. Despite this, some pairs failed to interact throughout the initial observation period (2 pairs in the first contest, 9 pairs in the second contest).

Each pair was observed continuously for 30 min after their first interaction. If no contact was made within 30 min of being placed in the contest arena, the observation was terminated. The number of aggressive, submissive, and neutral interactions that the focal male engaged in was recorded (Eggert et al. 2008). All data were recorded using iObserver application version 1.1 (Skware 2011, www.skware.com) for iPad.

After the initial observation period, contest arenas (containing males) were placed into an incubator at 21°C ($\pm 1^\circ\text{C}$) and sampled every 30 min to determine fight outcome. A winner was declared when one male was present on the carcass for 2 consecutive observations, and the other male was outside the inner ring. After a winner was determined, no further observations were made, and if no clear winner was seen after 3 h, observations ceased.

Statistical analysis

Only trials in which the focal male completed 2 contest trials resulting in clear outcomes were included in analyses. As a result, the original sample size of $n = 120$ per contest was reduced to $n = 73$ for each contest. Replicates were approximately evenly spread across treatments (OE = 19, ON = 19, YE = 17, YN = 18). All

analyses were conducted in R version 2.13.2 (R Development Core Team, 2012).

Prior to analyzing male contest behavior, we conducted principal component analysis to obtain composite measures that best described the axes of variation in male behavior. This analysis is highly suited to the analysis of contest behavior because it accounts for the covariance structure of multiple response variables and provides composite measures of behaviors that best describe the variation in the data (Jolliffe 2002). We included data on all types of interactions (aggressive, submissive, and neutral) between focal and nonfocal males from both first and second contests. This meant that the resulting principal components were comparable across a male's first and second contest. This analysis produced 2 vectors with eigenvalues greater than 1 (Table 1). The first principal component (PC1) described 44.0% of the variation in the data. All types of male encounters (aggressive, submissive, and neutral) loaded strongly and positively on this component, and thus, this vector represents "male encounter rate." The second principal component (PC2) described 25.5% of the variation in the data. High values of PC2 indicate males that engage in high numbers of aggressive encounters but low numbers of submissive encounters (neutral encounters did not load strongly on this component). Thus, PC2 effectively describes variation in the ratio of aggressive to submissive encounters, and hereafter, we refer to this vector as "male aggression."

To investigate the effects of male age and prior social experience on these 2 behavioral vectors, as well as on contest outcome, we analyzed data from each male's first contest using generalized linear models. Distributions of each response variable were determined from q-q plots and histograms. Male encounter rate was analyzed using a quasi-Poisson error distribution, and male aggression was analyzed using a Gaussian distribution. Contest outcome (i.e., winner or loser) was analyzed using a binomial distribution. Each model included male age and social experience treatment as fixed effects, relative male size (i.e., [focal male pronotum width – nonfocal male pronotum width]/focal male pronotum width) as a covariate, and all 2-way interactions (Briffa et al. 2013). Minimal adequate models were obtained by stepwise elimination of nonsignificant terms (Crawley 2007). We also analyzed our data including only contests where males differed in size by less than 0.5 mm because motivational effects are likely to play a greater role in individuals that are closely matched in size. These analyses gave qualitatively similar results to the full dataset, and so we present the results from our full dataset only here. The similarity of these results attests to the robustness of our conclusions. Furthermore, we investigated whether there were quadratic effects of relative size on contest behavior or outcome. As there were none, the results are not presented here.

To investigate the effects of male age and prior social experience on winner and loser effects, we analyzed data from each male's

second contest using generalized linear models. We used a similar approach as that outlined above for analyzing a male's first contest except that we also included the outcome of a male's first contest as a fixed factor. This allowed us to determine if there were any winner or loser effects (i.e., an effect of first contest outcome on any of our response variables), as well as whether male age or social experience mediated these winner–loser effects (i.e., any significant effects of the interactions between these treatments and outcome of a male's first contest on any of our response variables).

RESULTS

Effects of age, experience, and relative male size on contest behavior

Contrary to expectation, male age did not influence contest behavior. There were no main effects of age on either of our behavioral variables (male encounter rate: $F_{(1,70)} = 2.529$, $P = 0.1163$; male aggression: $F_{(1,69)} = 0.039$, $P = 0.844$). Male age did not influence contest behavior through any interactions with other terms included in the models (all interaction terms removed from the models at $P > 0.219$).

Social experience on the other hand did influence contest behavior. However, this was not via a significant effect on male aggression ($F_{(1,71)} = 3.010$, $P = 0.087$) as was predicted, but rather via a significant effect on male encounter rate ($F_{(1,71)} = 4.942$, $P = 0.029$). Males with prior social experience had higher encounter rates than naive males during their first contest (Figure 2). All interaction terms involving social experience were removed from the models ($P > 0.077$).

Neither male aggression nor male encounter rate were related to male relative size (aggression: $F_{(1,70)} = 0.924$, $P = 0.339$; encounter rate: $F_{(1,69)} = 1.285$, $P = 0.261$).

Effects of age, experience, and relative male size on contest outcome

Male relative size was the only term in our model that had a significant effect on the outcome of a male's first contest ($\chi^2_{(1,72)} = 13.178$, $P < 0.001$ (Figure 3a). Neither male age nor social experience had significant main effects on the outcome of a male's first contest (male age: $\chi^2_{(1,70)} < 0.006$, $P = 0.939$; social experience: $\chi^2_{(1,71)} = 1.533$, $P = 0.216$), nor did they influence contest outcome through any interaction effects (all interactions removed from the model at $P > 0.163$).

Effects of age, experience, and relative size on winner–loser effects

We found very little evidence for either winner or loser effects in this study. The outcome of a male's first contest did not influence the outcome of a male's second contest ($\chi^2_{(1,71)} = 0.936$, $P = 0.333$).

Table 1
Loading of male interactions on each principal component.

	Male encounter rate (PC1)	Male aggression (PC2)
Number of fights initiated	0.543	0.632
Number of chases initiated	0.134	0.828
Number of fights received	0.877	–0.296
Number of chases received	0.834	–0.305
Number of nonescalated contacts	0.651	0.093

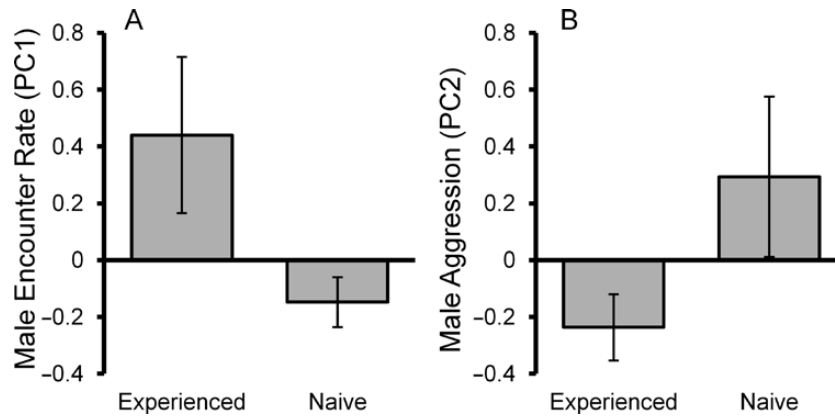


Figure 2

Effect of social experience on male contest behavior during a male's first contest. (A) Male encounter rate and (B) male aggressive behavior. Mean \pm standard error.

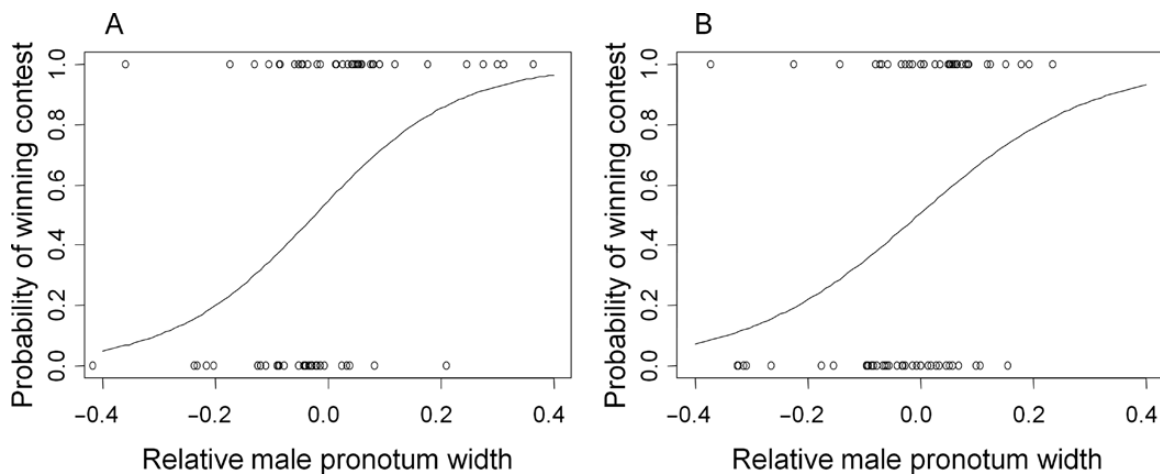


Figure 3

Logistic relationships showing the effect of relative pronotum width ($[\text{focal male} - \text{opponent}] / \text{focal male}$) on contest outcome. (A) A male's first contest and (B) a male's second contest. Mean \pm standard error.

We also found no evidence that winner or loser effects mediated the relationship between male relative size and contest outcome (i.e., the interaction between relative pronotum width and outcome of first contest was not significant: $\chi^2_{(1,65)} = 0.129$, $P = 0.7187$). Further, we found no evidence that male age or experience influenced the outcome of a male's second contest (male age: $\chi^2_{(1,70)} = 0.118$, $P = 0.739$; social experience: $\chi^2_{(1,69)} = 0.025$, $P = 0.875$) or that these factors mediated winner or loser effects (i.e., interactions involving these terms were dropped from the model at $P > 0.212$). The only term included in our model that predicted the outcome of a male's second contest was relative size ($\chi^2_{(1,72)} = 8.801$, $P = 0.003$).

Male contest behavior in the second contest was, however, influenced by the outcome of a male's first contest and by prior social experience. These factors interact to influence male encounter rate (interaction: $F_{(1,66)} = 5.522$, $P = 0.022$; fight 1 outcome: $F_{(1,66)} = 3.986$, $P = 0.050$; social experience: $F_{(1,66)} = 4.366$, $P = 0.041$) and similar to results from a male's first contest, do not influence male aggression. Experienced males that won their first contest had lower encounter rates than experienced males that had lost their first contest, whereas for naive males, there was no difference in behavior whether they won or lost their first contest (Figure 4). For male encounter rate, all other terms were dropped

from the model (all $P > 0.176$). For male aggression, all terms were dropped from our final model (all $P > 0.154$) leaving only the intercept.

DISCUSSION

Life-history theory predicts that individuals should increase investment in reproduction as their residual reproductive value decreases. In animals that compete for breeding resources, this could lead to increased aggression as individuals age (Kemp 2006). However, as individuals age, they also gain information on their relative status in the population, which may influence whether they are likely to engage in costly contest behavior and thus whether they are likely to dominate breeding resources. Recent theory regarding the effects of experience on contest behavior suggests that as an animal ages and gains experience, it should become less aggressive (Fawcett and Johnstone 2010). This is because older individuals have nothing to gain from escalating a contest they are unlikely to win, whereas younger individuals gain by learning about their relative status within the population. Here, we tease apart the often confounded effects of male age and social experience on male fighting behavior to test how these factors influence male contest behavior and

fighting ability exist, as may be the case when morphology correlates strongly with fighting ability.

The effects of experience on contest behavior that we see here do not support the idea that male burying beetles gain information on their relative competitive status through either social experience per se or through fighting experience more specifically. According to theory (Fawcett and Johnstone 2010), experienced individuals with information about their relative status in the population should be less aggressive than naive individuals and should be less responsive to winner effects than naive individuals. We found neither of these effects. This suggests that previous winner–loser effects found in burying beetles (Otronen 1990) may be due to changes in actual fighting ability, resulting perhaps from injury, rather than changes in perceived fighting ability. Or that the assessment strategy employed by males does not allow them to assess their own absolute RHP during interactions and then arrive at an estimate of their relative RHP in subsequent contests. Further studies investigating how experience alters subsequent contest behavior in the absence of potentially confounding physiological effects of winning and losing are needed to test whether self-perception of fighting ability has a general role to play in determining contest behavior.

If the effects of experience on behavior that we see here are not due to changes in perceived likelihood of winning contests, what could be their cause? The fact that both fighting experience and social experience per se influence the same behavior suggests it is not fighting itself that individuals are responding to but rather the fact that they have interacted with other individuals. Social experience is known to mediate many behavioral and physiological processes in animals. For instance, studies have shown that prior social experience can influence boldness (Frost et al. 2007; Edenbrow and Croft 2013) or stress hormones (Sachser et al. 2013). In addition, prior social experience may influence how individuals are perceived by others (Ruploh et al. 2013). Given the complexity of the possible effects of prior social experience on behavior, further investigation and manipulative experiments are required before we can interpret the specific effects that we see here.

An alternative explanation for our results is that rather than manipulating male self-perception of fighting ability, our social experience treatment may be manipulating male perception of population density. Previous work suggests that aggression is likely to be greatest at intermediate population densities (reviewed in Knell 2009). This is because under low population densities, males may redirect investment away from aggression toward mate searching, and under high population densities, males may redirect investment from aggression toward alternative mating strategies (Knell 2009). Our results show that experienced males had higher encounter rates during their first contest than naive males. This suggests that high encounter rates are not due to a switch toward mate searching resulting from male perception of low population density. To determine whether perception of population density influences contest behavior in this system would require further studies manipulating the number or frequency of individuals that a male encounters prior to contests.

CONCLUSIONS

Our male age and social experience treatments were designed to manipulate male residual reproductive value and perception of relative fighting ability within the population (respectively). Both of these factors are expected to influence male motivation to escalate contests rather than their ability to win contests. Motivation has been

suggested to influence contest behavior and outcome in many species (Bergman et al. 2010). However, there are few cases where effects on fighting ability can be ruled out altogether. Our results suggest that male motivation has little (if any) effect on contests in male *N. vespilloides*. We suggest that this is likely because body size is a strong predictor of success in competitive situations and high natural variation in this trait means that selection on factors that influence contest outcomes via changes in motivation is likely to be weak. Furthermore, in this species males may adopt alternative reproductive tactics that allow them to gain reproductive success even when they do not dominate a carcass. Our study highlights the need to place contest studies in an ecological context if we are to understand how variation in contest behavior evolves. In species where morphological traits (e.g., body size or weapon size) are strong predictors of fighting ability and where there is high variation in the size of such morphological traits in natural populations, then selection on factors that influence the motivation of individuals to engage in contests is likely to be weak. Thus, the only factors that are likely to influence contest outcomes are those that influence fighting ability itself.

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