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Aggressiveness and Size: A Model and Two Tests

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abstract: Individual variation in aggressive behavior in animals might be caused by adaptive covariation with body size. We developed a model that predicts the benefits of aggressiveness as a function of body size. The model indicated that individuals of intermediate sizes would derive the greatest benefits from being aggressive. If we assume that the cost of aggression is approximately uniform with respect to body size, selection should favor higher aggression in intermediate-sized individuals than in large or small individuals. This prediction was tested by stimulating male Madagascar hissing cockroaches, *Gromphadorhina portentosa*, with disembodied antennae and recording the males' aggressive responses. Antennae from larger males evoked weaker responses in subjects, suggesting that males obtained information about their opponents' size from the opponents' antennae alone. After accounting for this effect, we found support for the key prediction of our model: aggressiveness peaked at intermediate sizes. Data from actual male-male interactions validated that the antenna assay accurately measured aggressiveness. Analysis of an independent data set generated by staging male-male interactions also supported the prediction that intermediate-sized males were most aggressive. We conclude that adaptive covariation between body size and aggressiveness explains some interindividual variation in aggressiveness.

Keywords: aggression, behavioral syndromes, chemical communication, cockroach, *Gromphadorhina portentosa*, male-male competition.

Individual animals within a population vary with respect to their behavioral type. For example, one individual may consistently exhibit shy behavior whereas another consistently exhibits bold behavior (reviewed in Bell et al. 2009). Such variation is of great interest to behavioral ecologists because of its effects on fitness (reviewed in Smith and Blumstein 2008). Theoretical work indicates that an individual's optimal behavioral type (the type that will tend to result in the highest fitness) may depend on other characteristics of its bearer (Stamps 2007; Wolf et al. 2007). Interindividual variation in behavioral type might be maintained by individuals' adaptive responses to interindividual variation in size, growth rate, body condition, and other features.

We examined the relationship between aggression and body size. Consistent interindividual variation in aggressive behavior is likely to have important fitness consequences because aggression mediates competition for resources such as food, territory, social status, and access to mates (e.g., Duckworth 2006; While et al. 2009 and references therein). Individuals that express optimal levels of aggression stand to secure resources and gain the attendant fitness benefits (reviewed in Arnott and Elwood 2009). Those that express insufficient aggression will fail to secure resources that they would have secured were they more aggressive. Individuals that are overly aggressive, however, will incur costs (in terms of energy and injury) that exceed the benefits from the resources they gain. In addition to paying the high costs of fighting, overly aggressive individuals may also pay inherent costs of high aggression. These include costs associated with the proximate regulators of aggression (e.g., testosterone; Marler and Moore 1988) and behavioral trade-offs with aggression (Duckworth 2006).

In many species, body size contributes strongly to an individual's ability to win fights (i.e., its resource-holding potential; Parker 1974). The fitness benefits of aggressive behaviors depend on the degree to which those behaviors will help an individual win agonistic contests. If we define an individual's aggressiveness as its tendency to perform aggressive behaviors at a high rate in an agonistic contest, the benefits of aggressiveness should vary with respect to the actor's size. Variation in size could be maintained by several factors, including access to nutrition. We developed a model that predicts the optimal level of aggressiveness over a range of sizes.

Several classical models predict patterns of fight escalation as a function of contestants' relative resource-hold-

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ing potential (e.g., Enquist and Leimer 1983; Grafen 1987). Our model differs from those models because it attempts to predict consistent individual differences in an actor's aggressive behavior independent of its opponent's resource-holding potential (see also Taylor and Elwood 2003). A number of studies have shown rapid adaptive plasticity in aggression with respect to both the resources at stake and the opponent (reviewed in Arnott and Elwood 2008, 2009). The existence of rapid plasticity, however, does not rule out the possibility of individual differences. If rapid plasticity (on the order of seconds or minutes) in aggression is limited, selection may favor individuals that commit to a range of aggressiveness that optimizes fitness on average (Sih et al. 2004). For example, rapid plasticity in aggressiveness could be regulated by the activity level of certain endocrine organs, but the size of those organs (and thus their production capacity) may be determined by a longer-term developmental process. If this model is realistic, individuals could differ adaptively with respect to average aggressiveness and still exhibit rapid adaptive plasticity in response to environmental factors.

We tested our model with males from a laboratory population of Madagascar giant hissing cockroaches, *Gromphadorhina portentosa*. The social system of this species has been described as involving dominance (Clark and Moore 1995; Guerra and Mason 2005) and dominance-based territoriality (Leibensperger et al. 1985), but observational studies of natural colonies are lacking. In captivity, male hissing cockroaches fight frequently (Barth 1968). During fights, males repeatedly butt one another with the large bumps on their pronota. Size is a strong predictor of fight outcome (Barth 1968; Clark and Moore 1995). Individual male hissing cockroaches exhibit consistent differences in aggressiveness (Logue et al. 2009). Dominant males achieve greater mating success than do submissive males in a standardized male-male-female interaction experiment (Clark 1998).

The outcomes of previous fights affect an individual's aggressiveness in many species (Dugatkin 1997). Clark et al. (1995) did not find that winning or losing a fight affected a male hissing cockroach's propensity to dominate a novel opponent in the future. That study, however, does not allow us to rule out the possibility of winner or loser effects in this species because the sample size was not very large and its design does not allow the comparison of aggression in winning and losing males to that in matched naive controls. In this study, we sidestepped the potentially confounding effects of winning and losing by using individuals that had not experienced winning or losing fights. We attempted to maintain subjects' naïveté through replicated measurements of aggression by stroking subjects with disembodied antennae and measuring their behavioral responses (Chou et al. 2007; While et al. 2009). This technique also allowed us to control the interaction between the stimulus and the subject at a level that would be impossible to achieve in a staged interaction between two living males.

This study consists of four parts. First, we developed a model that predicts optimal levels of aggressiveness as a function of body size. Second, we tested for the predicted relationship in our laboratory population of hissing cockroaches by using a chemotactile stimulation test that we call the "antenna assay." Third, we attempted to validate the antenna assay as a reliable assay for measuring aggression. Finally, we tested the model's prediction on an independent data set from a prior study.

Methods

The Model

We generated an optimality model of aggression. In our model, an actor competes with opponents from its population. Actors' sizes ranged from 0.1 to 0.9 in increments of 0.1. We ran simulations with three different levels of aggression (0.1, 0.3, and 0.5). Aggression was modeled as a bonus to an actor's fight strength: a nonaggressive actor's fight strength was simply its size, but an aggressive actor's fight strength was its size plus its aggression. Actors interacted at random with opponents from a population characterized by a Gaussian distribution of sizes ($\text{mean} = 0.5$, $\text{SD} = 0.2$). Opponents' fight strengths were calculated in the same way as were actors'. In a given run of the model, all aggressive individuals had the same level of aggression. It was, however, possible for the actor to be aggressive and the opponent to be nonaggressive or vice versa. We simulated populations of opponents with various frequencies of aggressiveness (0.0, 0.1, 0.5, 0.9, and 1.0). When the frequency of aggression in the population was less than 1, a random process determined whether a given opponent was aggressive. For each simulated interaction, the focal individual's fight strength was compared to the opponent's fight strength. If the focal individual's fight strength was higher than that of its opponent, the focal individual won. If it was lower, the focal individual lost.

We ran two simulations for every permutation of values of the three parameters (focal size, level of aggression, and frequency of aggressiveness). Each simulation consisted of 10,000 iterations. In the first simulation, the focal individual was not aggressive, and in the second, it was. We subtracted the proportion of fights won without aggression from the proportion won with aggression to determine the benefit of aggression. Simulations were conducted in Microsoft Excel 2007 (Microsoft, Redmond, WA) running the PopTools 3.1.1 add-in (Hood 2009). The simulation model is available as a zip file in the online edition of the *American Naturalist.*

Antenna Assay

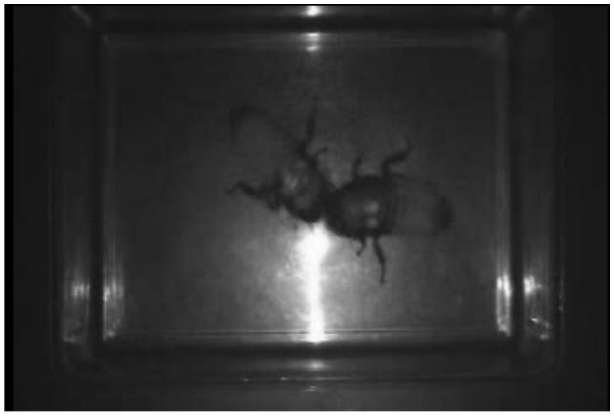
The model can be used to generate a predicted relationship between size and aggressiveness (see "Results"). We tested this prediction on males from a laboratory colony of hissing cockroaches. Males of this species are appropriate subjects for this study because they exhibit high variance in body size, fights between males are common, and previous work indicated that males vary with respect to aggressiveness (Logue et al. 2009). Males were born at the University of Lethbridge in breeding colonies, which were founded by animals purchased from VWM Reptiles (Edinburg, IL). Male nymphs were placed in all-male nymph colonies shortly after they began to exhibit sexually dimorphic subgenital plates. On reaching the adult molt (indicated by distinctive humps on the pronotum and feathered antennae), males were weighed, measured, and isolated in plastic boxes (21 cm long × 14 cm wide × 10 cm high). We used digital calipers (Mitutoyo SC-6″) to measure the maximum length and maximum width of the pronotum. All animals were maintained in a 12 : 12 reversed light-dark cycle at 28°C and 50% humidity. Animals had ad lib. access to water, dog chow, and sections of carton egg crates that they used for shelter. Dog chow (Purina Dog Chow; Nestlé Purina PetCare, St. Louis, MO) was ground in a food processor, mixed with water, formed into ~1-cm-thick cakes, and allowed to dry before being fed to the animals. Isolated males received 1 g of peeled carrot each week.

The antenna assay involved two classes of males: donor males ($N = 86$) donated antennae to be used as stimuli and focal males ($N = 57$) comprised our pool of test subjects. Donors were adult males that had been subjects in a previous experiment (Mishra et al. 2011). Only males with two normal antennae were used as donors. Before preparing stimuli, we measured the width and length of each donor's pronotum. We then placed the donor in a covered plastic cup, which went into a freezer until the male stopped moving (~4 min). Workers wore clean latex gloves during antenna removal and stimulus preparation and were careful not to allow antennae to touch potentially contaminated surfaces. Clean surgical scissors were used to cut off the males' antennae at their base. Donor males were then euthanized by freezing. Each antenna was taped to a balsa wood stick with clear tape, such that the distal end of the antenna was distal to the stick and ~90% of the antenna hung off the end of the stick. Each donor male produced two stimuli. Antennae were allowed to reach room temperature before use.

It was important to demonstrate that males were responding to the antenna stimuli with aggression rather than irritation in response to being stroked with a foreign object. We therefore fashioned control stimuli from feather shafts that had physical characteristics (size, shape, and flexibility) similar to those of hissing cockroach antennae but that lacked the antennae's chemical properties. We first removed the barbs from an appropriately sized chicken feather and trimmed the shaft to the average length of a male antenna (30 mm). Feather shafts were attached to balsa wood sticks with clear tape as above.

Each focal male was subjected to four randomly ordered trials: in three antenna trials, he was stroked with a donor male's antenna, and in one control trial, he was stroked with a feather shaft. Each trial was separated by at least 3 days. Before a trial, the focal male was placed, in his box, in a dark room heated to 28°C. The lid and all contents were removed from the box, and the walls were lubricated with a mixture of petroleum jelly and mineral oil to prevent escape. The male was then left to acclimate for 5 min. All trials were video-recorded from above with a Sony Handicam DVD 103 in night-vision mode (Sony Electronics, San Diego, CA). In this mode, the camera emits and receives near-infrared light. Sample videos (videos 1, 2) are available in the online edition of the *American Naturalist.*

During the trial, an experimenter stroked the focal male with the donor male's antenna or the control stimulus. Standardization was achieved by listening to an MP3 recording on headphones. The recording consisted of vocal cues and clicks that told the experimenter where and when



Video 1: Still photograph from a video (video 1, available in the online edition of the *American Naturalist*) depicting two male hissing cockroaches fighting under near-infrared illumination. The video sequence shows several examples of butting, in which one male rams the other with the bumps on his pronotum. The male that does the butting also exhibits the behavior "abdomen thrash," which may serve as a vibrational signal.

Video 2: Still photograph from a video (video 2, available in the online edition of the *American Naturalist*) depicting a male hissing cockroach responding to being stroked with a disembodied antenna taped to a stick. In the video, the male exhibits behaviors that are typical of aggressive encounters, including "butt" and "abdomen thrash."

to stroke the male, respectively. The recording instructed the experimenter to stroke the subject's body 10 times, its antennae 10 times, its body 10 more times, and its posterior 10 times. Consecutive strokes to a given region of the body were separated by 0.5 s. Strokes to the body ran along the longitudinal access, in an alternating anterior-posterior pattern. Strokes to the antennae and the animal's posterior area were perpendicular to the body axis, in an alternating right-left pattern. The entire recording was repeated 10 times. Trials lasted 250 s.

Validating the Antenna Assay

Males that completed all four trials were size-matched to form dyads based on the size index (pronotum width × pronotum length; average size difference between dyads, 13.0%; maximum, 34.9%). We call this index "pronotum area" because the pronotum is approximately rectangular. In this species, pronotum area is a more stable measure of size than is body weight (D. M. Logue, unpublished data). We conducted male-male interactions at least 3 days after both dyad mates finished their last trial. After a 5-min acclimation period, dyad mates were simultaneously placed in a plastic box (the same kind of box used in the antenna assay), and their antennae were made to touch. They were then allowed to interact for 15 min.

Analysis

Videos of all trials were analyzed with the program JWatcher 1.0 (Blumstein et al. 2006). The observer recorded each instance of butting behavior by the focal male. Butting occurs when a male lowers his head and rushes forward (e.g., Logue et al. 2009). In an actual fight, this would usually result in him striking and pushing his opponent. Although males exhibited several different aggressive behaviors, we chose to focus on butting because (1) this is the most commonly used attack in the male hissing cockroach's repertoire (Clark and Moore 1994), making it most amenable to statistical analysis; (2) a quantitative analysis of hissing cockroach fights concluded that butting and lunging (which we counted as butting) are the most aggressive behaviors in males' repertoires (Clark and Moore 1994); and (3) analyses using multiple variables subjected to principal components analysis produced results qualitatively similar to those of analyses using only "butt."

We first tested whether stroking males with an antenna elicited higher levels of aggressive behavior than did stroking with a feather shaft. The variable "butts" was not normally distributed, so we used rank-based analyses for hypothesis tests involving butts. We used Wilcoxon signed-rank tests to compare the average number of butts in a male's antenna trials to the number of butts in his control trial.

We used a Spearman rank correlation to determine whether the mean size of the donor male affected the focal male's mean butting response (using the averages was a conservative choice that avoids the problem of pseudoreplication). When we found that it did, we ran a linear regression in which the donor male's size predicts the focal male's butt with each trial as a separate datum point to generate residual butting scores for further analysis (see "Results"; although we do use a parametric test here, it is not for the purpose of hypothesis testing but rather to generate residuals). The response variable "butt" was log transformed before analysis to better conform to the assumption of normality. We wanted to know the repeatability of butting behavior during antenna trials, so we calculated the intraclass correlation coefficient ("repeatability") of residual butting accounting for variability in trial numbers among males and its approximate confidence interval (Becker 1984, pp. 37–43; Lessells and Boag 1987; Bell et al. 2009). We then ran a Kruskal-Wallace test to test the null hypothesis that all individuals express equal median levels of residual butting and a Friedman test to look for order effects. Quadratic regression was used to determine whether a focal male's size predicted his mean residual butting, as predicted by our model. The variable "mean residual butt" was normally distributed, justifying the use of parametric statistics.

We attempted to validate our aggression assay by comparing the results of that assay to data gathered during actual contests between males (as in D'Eath 2002). Dyad mates' behaviors during a male-male interaction trial are not independent of one another, so the interaction trial (rather than individual) was the experimental unit for this analysis. We haphazardly defined one male in each dyad as the focal male and the other as the opponent and then subtracted the opponent's value from the focal male's value to generate compound variables for mean residual butting during antenna trials and butting during the male-male interaction. We constructed a linear regression in which the first variable was treated as independent and the second as dependent.

Some males died before we could complete all of the assays. We did not consider data from males that died before completing at least three trials (either two antenna trials and a control or three antenna trials). The final data set included 166 antenna trials and 56 control trials from 57 males. We conducted the locally weighted scatterplot smoothing (LOESS) analysis in SAS 9.1.4 (SAS Institute, Cary, NC) and all other statistical tests in SPSS 17.0.0 (SPSS, Chicago).

Testing the Model with an Alternative Data Set

We tested the prediction that intermediate-sized males are most aggressive by using a data set generated by pitting an individual focal male against a size-matched opponent in the focal male's home cage for 15 min and counting the number of focal male butts (see Logue et al. 2009 for details). In 16 of the 70 interactions, neither male butted or exhibited other aggressive behavior. We excluded those interactions from the data set because the animals did not engage in an agonistic contest. On average, the pronotom area of size-matched males differed by 2.3%, with a maximum difference of 27.5%. The focal males used in this study were different individuals from those used in the antenna assay. We log transformed the variable "butts" before analysis to conform to the assumption of normality.

Results

The Model

Subtracting the proportion of fights won without aggression from the proportion won with aggression generated a hump-shaped curve describing the benefits of aggression over the range of sizes (fig. 1). The shape of the curve varies with both the level of aggression and the frequency of aggression in the population (fig. 2). Specifically, (1) the benefits of aggression increase with the level of aggression, (2) the size class that reaps maximum benefits increases with the frequency of aggression in the population (fig. 3), and (3) the effect size of result 2 increases with the level of aggression. Nevertheless, under all of the parameter sets, actors of intermediate body size gained greater benefits from aggression than did actors of extreme sizes (as evidenced by the fact that all points in fig. 3 fall between 0 and 1).

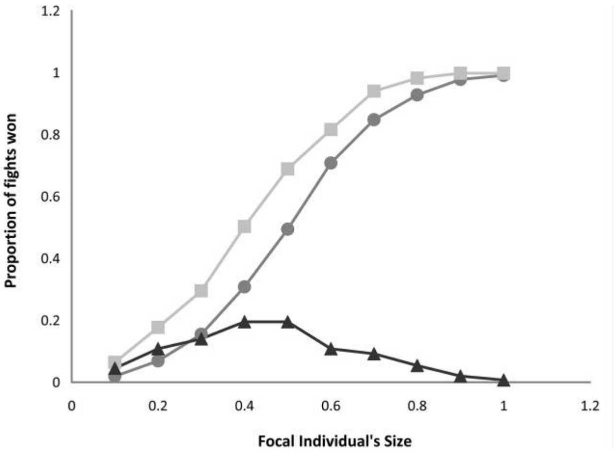


Figure 1: Results of a simulation model in which focal individuals of various sizes engage in contests with other individuals chosen at random from a population with a normal size distribution. The plot shows the proportion of fights that focal individuals are predicted to win if they are nonaggressive (*circles*) or aggressive (*squares*), as well as the difference in these two values, which we term the "benefit of aggression" (*triangles*). These data were generated with the following parameters: frequency of aggression = 0.0; effect of aggression = 0.1.

Antenna Assay

On average, males butted almost seven times as frequently during antenna trials as they did during control trials (average ± SD: antenna = 8.28 ± 8.43, control = 1.20 ± 2.99; median (interquartile range): antenna = 5 (6.3), control = 0 (0); Wilcoxon signed-rank test: $Z = -5.33$, $N = 56$, $P < .001$). The average donor male's size (pronotum area) was negatively correlated with the focal male's average butting response (Spearman rank correlation: $\rho = -0.264$, $N = 57$, $P = .048$). We generated residual levels of butting to draw out some of the variation attributable to donor size. We wanted to allow for the possibility that the relationship between donor size and butting response was nonparametric, so we developed LOESS models, relying on the bias-corrected Akaike Information Criterion (AICc) to choose the optimal smoothing parameter. The lowest (best) AICc was achieved with very high levels of smoothing. Since high smoothing produces a nearly straight line, we opted to base our residuals on a simple linear regression.

The intraclass correlation coefficient, or repeatability (r), of residual butt was 0.331 (approximate 95% confi-

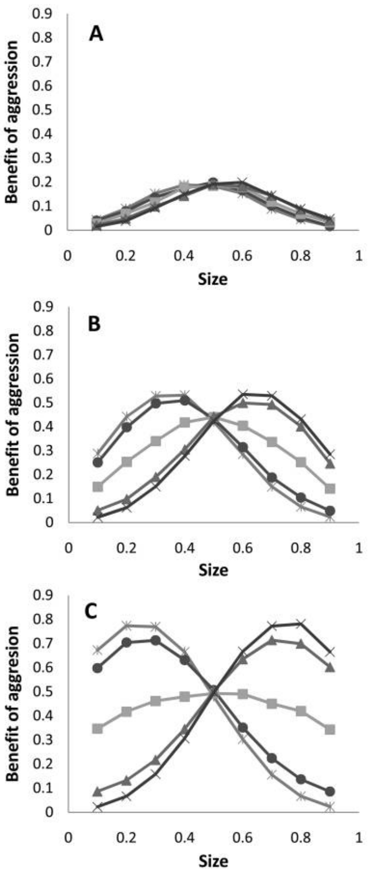


Figure 2: Predicted benefits of aggression over a range of body sizes. The three graphs represent three levels of aggression (*A*, 0.01; *B*, 0.3; *C*, 0.5). Within each graph, we plotted the expected distribution of benefits versus size over a range of frequencies of aggression (*asterisks* = 0.0; *circles* = 0.1; *squares* = 0.5; *triangles* = 0.9; *crosses* = 1.0).

dence interval: 0.163–0.502). A Kruskal-Wallace test showed that males differed in residual butting at levels that exceeded chance ($\chi^2 = 86.64$, df = 56, $P = .005$). A nonparametric alternative to a repeated-measures ANOVA revealed no evidence of an order effect among antenna trials (Friedman test: $N = 52$, $\chi^2 = 2.46$, df = 2, $P = .29$). We determined the mean level of residual butt for each focal male. Mean residual butt was normally distributed, justifying the use of parametric statistics on these data. We ran both linear and parametric models and then compared their goodness of fit using the Akaike Information Criterion (AIC). Lower AIC values indicate better model fit (Burnham and Anderson 2002). The linear regression of mean residual butt against pronotum area was not statistically significant ($r^2 = 0.03$, $F_{1,55} = 1.69$, $P = .199$, AIC = 66.47), but the quadratic regression was ($r^2 = 0.121$, $F_{1,54} = 3.72$, $P = .031$, AIC = 62.83; fig. 4*A*). The difference between the AIC values of the two models (ΔAIC = 6.25) exceeded 2, indicating that the linear model was not well supported relative to the quadratic models (Burnham and Anderson 2002, p. 70). The quadratic model estimated peak aggression at pronotum area = 270 mm^2 (sixty-fourth percentile).

Validating the Antenna Assay

The results of our aggression assay predicted aggressive behavior in actual male-male contests. Specifically, the difference between the average number of butts during dyad males' antenna trials predicted the difference in the number of butts during their interactions (linear regression: $F_{1,24} = 5.64$, $r^2 = 0.19$, $P = .026$). One pair was excluded from this analysis because it did not produce any butts.

Testing the Model with an Alternative Data Set

When we regressed butt on pronotum area by using the data set from Logue et al. (2009), we found that the linear regression was not significant ($r^2 = 0.001$, $F_{1,51} = 0.052$, $P = .821$, AIC = 91.87) but the quadratic regression was ($r^2 = 0.145$, $F_{1,50} = 4.24$, $P = .020$, AIC = 85.62; fig. 4*B*). The disparity between the AIC values (ΔAIC = 3.64) exceeded 2, indicating that there was better support for the quadratic model. The quadratic model estimated peak aggression at pronotum area = 251 mm^2 (forty-first percentile).

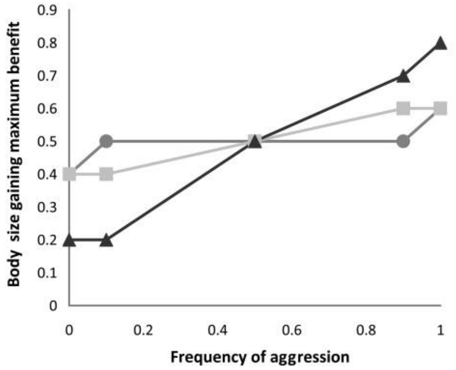


Figure 3: Size classes that our model predicted would receive the maximum benefit from exhibiting aggression over a range of frequencies of aggression in the population. Each line represents a different level of aggression (*circles* = 0.1; *squares* = 0.3; *triangles* = 0.5).

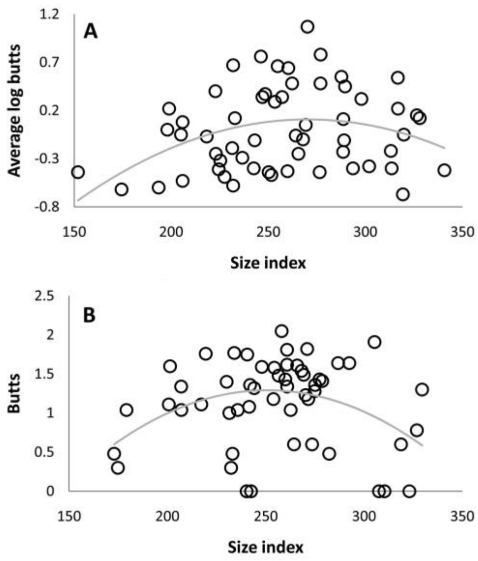


Figure 4: Distribution of aggressive butting versus body size in male hissing cockroaches. These plots show (*A*) the mean residual butting from three replicates of a chemotactile stimulation experiment and (*B*) the number of butts during an interaction with another male. Butts were log transformed. The *Y*-axis in *A* indicates the average residual from a linear regression of log butts on donor size.

Discussion

We modeled aggressiveness as a trait that interacts with size to influence the probability that an individual will win a contest. Our model suggests that, all things being equal, individuals that compete aggressively for resources should exhibit variable levels of aggressiveness, with intermediate-sized individuals being more aggressive than large or small individuals. Consistent with the first part of this prediction, aggressiveness varies among individual male hissing cockroaches. A recent meta-analysis of the repeatability of behavior found that aggression was the second most repeatable class of behaviors, with an average repeatability of $r = 0.33$ (Bell et al. 2009). Apparently, male hissing cockroaches ($r = 0.33$) are not exceptional with respect to the repeatability of aggressive behavior.

Consistent with the second part of our model's prediction, aggression peaked among intermediate-sized males in both of our data sets (sixty-fourth and forty-first percentiles of pronotum areas, respectively). These findings support key predictions of the hypothesis that interindividual variation in naive aggression covaries adaptively with body size in our laboratory population of *Gromphadorhina portentosa*. More broadly, our model and its test provide support for the hypothesis that repeatable individual variation in behavior may be maintained by adaptive plasticity in response to constrained aspects of the phenotype, such as body size.

Although the model correctly predicted that aggression would peak in middle-sized actors, quadratic regressions explained only 12.1% and 14.5% of the variation in aggression in our two data sets. One explanation for the relative weakness of the pattern is that there may have been uncontrolled variation in the stimuli or in individual differences in aggression beyond those related to body size. Additionally, the quadratic regression may not have been the best model to fit (e.g., see the shape of the "benefit of aggression" curve in fig. 1). Without the ability to accurately parameterize the model, however, we chose the quadratic regression for its simplicity and its ability to test the model's key prediction.

A previous study that attempted to link aggression to body size in *G. portentosa* groups revealed no relationship between body size and butting, even though curvilinear relationships were considered (Clark and Moore 1994). Interestingly, that study did find that the aggressive behaviors "abdomen thrash" and "agonistic hiss" were expressed most strongly by middle-weight males. One potentially important difference between Clark and Moore's (1994) study and our own is that the males in their study were observed in social groups of five or 10 males, so each male's experience was much more variable than it was in our experiment. Further, the social interactions in their experiment might have masked certain individual tendencies (e.g., by generating winner or loser effects). Studies on pigs have found no relationship between size and aggression, although it is not clear that curvilinear relationships were considered in those studies (D'Eath and Pickup 2002; Bolhuis et al. 2005).

The key prediction of our model emerges from the assumption that there are more intermediate-sized individuals than either large or small individuals. We assume that only interactions with individuals of a size similar to that of the focal individual are affected by the occurrence of aggression in one or both individuals. For example, a very large individual will always beat a very small individual, even if the small individual is aggressive and the large one is not. Since we assumed a Gaussian size distribution, the proportion of opponents for whom fight outcome would depend on aggression is larger for intermediate-sized individuals than for either large or small individuals. The model should not be applied to populations in which the size distribution does not peak at an intermediate value.

Up to this point, we have assumed that the cost function of aggression is approximately flat across the size distribution, making the payoff function of aggression equivalent to the benefit function. A more realistic understanding of the cost function is a requirement for more precise estimates of the benefits of aggression. It is possible that the cost of aggression covaries with size in some species. Given the assumptions of our model, however, medium-sized males are expected to express the highest levels of aggressiveness unless the cost function were so biased toward extreme-sized individuals that it overwhelmed the effect of size on the benefit of aggression (fig. 2).

Although we modeled various levels of aggression, we did not allow individuals to flexibly express higher or lower levels of aggression. Modeling continuous aggression, however, would have required us to make assumptions about the cost function of aggression within a given size (this is different from our assumption that the cost of aggression is flat across sizes). Although this would be an interesting exercise, it would complicate the model a great deal. It is unlikely that individuals fight other individuals at random with respect to body size, but this violation probably has little effect on the validity of our model. If a potential opponent avoids a fight because it will probably lose, the actor can still reap the benefits of winning. Further, the benefit of aggressiveness comes from beating individuals of similar size, which would be unlikely to avoid a fight based on size alone.

The currency of our model is the proportion of interactions that an individual wins. This currency is appropriate only if by winning more interactions all individuals can expect to gain fitness. This would not be the case if, for example, only the most dominant 1% of individuals reproduced or if the social dominance of an individual has no bearing on its reproductive success (e.g., Engh et al. 2002). In hissing cockroaches, dominance appears strongly to influence mating success, but subordinate individuals can achieve some reproductive success in controlled trials (Clark 1998), suggesting that the currency of the model is appropriate to this system. We suggest that our model might be productively applied to systems in which winning fights can be expected to increase fitness in an approximately linear fashion.

The antenna assay developed by Chou et al. (2007) and modified in this study is a useful way to measure aggression in hissing cockroaches. We suggest that this kind of assay may be successfully applied other cockroaches and perhaps other fighting insects (e.g., crickets) to make controlled measurements of aggression.

Our analyses showed that the size of the donor was negatively correlated with the intensity of the focal male's response. Since large donors have large antennae, there is a positive correlation between the donor's size and the amount of stimulation that must have been overcome by some other effect to produce the negative relationship between donor size and response. We propose that this effect is the focal male's ability to assess an opponent's size by his antenna alone. Surface pheromones and the size of the antenna functionally communicate information about the opponent's size. Although this finding was not predicted by our model, which is blind to the opponent's resource-holding potential, it is certainly compatible. We agree with Clark et al. (1995), who suggest that olfactory cues may be involved in establishing dominance relationships between unfamiliar individuals, and call for further studies to elucidate the role of chemical communication during aggressive interactions in this species. A useful first step would be an experiment aimed at determining the relative role of chemicals and antenna size in assessing opponent size.

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Literature Cited

Arnott, G., and R. W. Elwood. 2008. Information gathering and decision making about resource value in animal contests. Animal Behaviour 76:529–542.

———. 2009. Assessment of fighting ability in animal contests. Animal Behaviour 77:991–1004.

Barth, R. H. 1968. The mating behavior of *Gromphadorhina portentosa* (Schaum) (Blattaria, Blaberoidea, Blaberidae, Oxyhaloinae): an anomalous pattern for a cockroach. Psyche 75:124–131.

Becker, W. A. 1984. Manual of quantitative genetics. 4th ed. Academic Enterprises, Pullman, WA.

Bell, A. M., S. J. Hankinson, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis. Animal Behaviour 77: 771–783.

Blumstein, D. T., J. C. Daniel, and C. S. Evans. 2006. JWatcher 1.0: an introductory user's guide. http://www. jwatcher.ucla.edu.

Bolhuis, J. E., W. G. P. Schouten, J. W. Schrama, and V. M. Wiegants. 2005. Individual coping characteristics, aggressiveness and fighting strategies in pigs. Animal Behaviour 69:1085–1091.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. 2nd ed. Springer, New York.

Chou, S.-Y., Z. Y. Huang, S.-C. Chen, R.-L. Yang, and R. Kou. 2007. Antenna contact and agonism in the male lobster cockroach, *Nauphoeta cinerea.* Hormones and Behavior 52:252–260.

Clark, D. C. 1998. Male mating success in the presence of a conspecific opponent in a Madagascar hissing cockroach, *Gromphadorhina portentosa* (Dictyoptera: Blaberidae). Ethology 104:877–888.

Clark, D. C., and A. J. Moore. 1994. Social interactions and aggression among male Madagascar hissing cockroaches (*Gromphadorhina portentosa*) in groups (Dictyoptera: Blaberidae). Journal of Insect Behavior 7:199–215.

———. 1995. Genetic aspects of communication during male-male competition in the Madagascar hissing cockroach: honest signaling of size. Heredity 75:198–205.

Clark, D. C., D. D. Beshear, and A. J. Moore. 1995. Role of familiarity in structuring male-male social interactions in the cockroach *Gromphadorhina portentosa* (Dictyoptera: Blaberidae). Annals of the Entomological Society of America 88:554–561.

D'Eath, R. B. 2002. Individual aggressiveness measured in a resident-intruder test predicts the persistence of aggressive behaviour and weight gain of young pigs after mixing. Applied Animal Behaviour Science 77:267–283.

D'Eath, R. B., and H. E. Pickup. 2002. Behavior of young growing pigs in a resident-intruder test designed to measure aggressiveness. Aggressive Behavior 28:401–415.

Duckworth, R. A. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. Behavioral Ecology 17:1011–1019.

Dugatkin, L. A. 1997. Winner and loser effects and the structure of dominance hierarchies. Behavioral Ecology 8:583–587.

Engh, A. L., S. M. Funk, R. C. Van Horn, K. T. Scribner, M. W. Bruford, S. Libants, M. Szykma, L. Smale, and K. E. Holekamp. 2002. Reproductive skew among males in a female-dominated mammalian society. Behavioral Ecology 13:193–200.

Enquist, M., and O. Leimer. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. Journal of Theoretical Biology 102:387–410.

Grafen, A. 1987. The logic of divisively asymmetric contests: respect for ownership and the desperado effect. Animal Behaviour 35: 462–467.

Guerra, P. A., and A. C. Mason. 2005. Information on resource quality mediates aggression between male Madagascar hissing cockroaches, *Gromphadorhina portentosa* (Dictyoptera: Blaberidae). Ethology 111:626–637.

Hood, G. M. 2009. PopTools, version 3.1.1. http://www.cse.csiro.au/poptools/.

Leibensperger, L. B., F. A. Traniello, and J. M. Fraser. 1985. Olfactory cues used by female *Gromphadorhina portentosa* (Dictyoptera: Blaberidae) during mate choice. Annals of the Entomological Society of America 78:629–634.

Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116–121.

Logue, D. M., S. Mishra, D. McCaffrey, D. Ball, and W. H. Cade. 2009. A behavioral syndrome linking courtship behavior toward males and females predicts reproductive success from a single mating in the hissing cockroach, *Gromphadorhina portentosa*. Behavioral Ecology 20:781–788.

Marler, C. A., and M. C. Moore. 1988. Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. Behavioral Ecology and Sociobiology 23:21–26.

Mishra, S., D. M. Logue, I. O. Abiola, and W. H. Cade. 2011. Developmental environment affects risk-acceptance in the hissing cockroach. Journal of Comparative Psychology (forthcoming).

Parker, G. A. 1974. Assessment strategy and the evolution of animal conflicts. Journal of Theoretical Biology 47:223–243.

Sih, A., A. M. Bell, J. C. Johnson, and R. E. Ziemba. 2004*a*. Behavioral syndromes: an integrative overview. Quarterly Review of Biology 79:241–277.

Smith, B. R., and D. T. Blumstein. 2008. Fitness consequences of personality: a meta-analysis. Behavioral Ecology 19:448–455.

Stamps, J. A. 2007. Growth-mortality trade-offs and "personality traits" in animals. Ecology Letters 10:355–363.

Taylor, P. W., and R. W. Elwood. 2003. The mismeasure of animal contests. Animal Behavior 65:1195–1202.

While, G. M., D. L. Sinn, and E. Wapstra. 2009. Female aggression predicts mode of paternity acquisition in a social lizard. Proceedings of the Royal Society B: Biological Sciences 276:2021–2029.

Wolf, M., G. S. van Doorn, O. Leimar, and F. J. Weissing. 2007. Life-history trade-offs favour the evolution of animal personalities. Nature 447:581–585.

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Two male giant hissing cockroaches (*Gromphadorhina portentosa*) square off. Photograph by Andrew Hurly.