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# Social Interactions and Aggression Among Male Madagascar Hissing Cockroaches (*Gromphadorhina portentosa*) in Groups (Dictyoptera: Blaberidae)

**Deborah C. Clark[1,2] and Allen J. Moore[1]**

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*We studied agonistic interactions among male Madagascar hissing cockroaches,* Gromphadorhina portentosa, *in groups of five (low-density) or 10 (high-density) males. Consistent with previous studies of male pairs, we observed aggression (Abdomen Flick, Abdomen Push, Butt, Lunge), submission (Crouch, Retreat), and noncontact behavior (Abdominal Extension, Abdomen Thrash, Agonistic Hiss, Stilt). Males at both densities performed all acts. However, males in the high-density group performed Abdomen Push significantly more often than males at a low density. The rate of each remaining act was unaffected by density. Regardless of density, males within social groups varied in aggression. More aggressive males utilized frontal assaults (Butt and Lunge) during interactions, while males displaying lower levels of aggression preferentially used the abdomen during interactions. More aggressive males performed Abdomen Flick more frequently, while males displaying lower levels of aggression performed Abdomen Push. We also investigated the relationship between male aggression and the four noncontact behaviors. We found that Abdominal Extension, Abdomen Thrash, and Agonistic Hiss were positively correlated with our aggregate measure of male aggression suggesting these are aggressive displays. Stilt was positively correlated with measures of both aggression and submission, leaving its function unclear. None of the behavioral acts examined in this study were highly correlated with male weight. Our results are discussed in light of possible hypotheses addressing the function of specific behavior during male–male competition.*

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**KEY WORDS:** male–male competition; agonism; *Gromphadorhina portentosa*; density; social display.

[1] Department of Entomology, Center for Evolutionary Ecology, University of Kentucky, Lexington, Kentucky 40546.

[2] To whom correspondence should be addressed at Department of Entomology, S-225 Agriculture Science Center North, University of Kentucky, Lexington, Kentucky 40546-0091.

# INTRODUCTION

Among animals living in structured social systems individuals must be able to distinguish accurately between dominant and subordinate group members to avoid unnecessary and potentially costly contests (Barnard and Burk, 1979). One mechanism for minimizing overt fighting is the use of threats and displays (Smith, 1977; West-Eberhard, 1979, 1983; Hauser and Nelson, 1991). Ritualized displays are often used to provide information about fighting ability and thereby allow individuals involved in social competition to adjust their behavior without continuous or prolonged physical combat (West-Eberhard, 1979, 1983; Maynard Smith, 1982; Huntingford and Turner, 1987).

Displays used as social signals are typically highly stereotyped, repetitive, and exaggerated to improve the function and emphasize the importance of the signal (Smith, 1977; Krebs and Dawkins, 1984; Krebs and Davies, 1987). Social signals are not expected to vary in form but they often vary in frequency. This variation may result from changes in population density (Borgia, 1981; Huntingford and Turner, 1987; Moore, 1987) or may reflect attributes of the displaying individual, such as ontogeny (Bekoff, 1981), body size (Maynard Smith and Brown, 1986), or other correlates of status (Krebs and Dawkins, 1987; Maynard Smith and Harper, 1988).

Our intention was to describe conditions that contribute to variation in social behavior in *Gromphadorhina portentosa*, a large wingless cockroach species from Madagascar. The most notable features of this species are the aggressive behavior of males, the use of complex acoustic signals and behavioral displays, and the sexually dimorphic pronotal horns. The social system of *G. portentosa* has been described as dominance-based territoriality with female mate choice (Leibensperger *et al.*, 1985). The agonistic repertoire of males is characterized by distinctive hissing accompanied by stereotyped behavior (Barth, 1968; Nelson and Fraser, 1980; Breed *et al.*, 1981; Leibensperger *et al.*, 1985). In dyads, hissing (Nelson and Fraser, 1980) and male size (Barth, 1968) are predictive of winning. Thus, although the conspicuous features of agonistic behavior in this species have been described, no studies have documented variation in aggression among individuals. In addition, previously published studies have focused on describing the behavior of pairs of *G. portentosa* males (Nelson and Fraser, 1980; Breed *et al.*, 1981). Although the behavior observed in dyads may reflect aspects of behavior in larger groups, studies of groups of males should provide additional insights into the social behavior of *G. portentosa*. Finally, a number of behaviors have been noted that occur during male–male competition but have not been assigned a function in the outcome of aggressive encounters (Breed *et al.*, 1985).

In this study, we documented the details of social behavior among groups of male *G. portentosa*. After describing the various acts that occur in social interactions, we determined when rates of behavior within newly formed social groups became stable. Second, since population density is known to influence aggression in other cockroach species (Ewing, 1972; Breed and Byers, 1979; Gorton *et al.*, 1979; Gautier *et al.*, 1988), we determined how male density affected the diversity and frequency of agonistic behavior in stable social groups. Third, we described interindividual variation in male aggression and determined if noncontact behavior that occurred during agonistic interactions was related to male aggression. Finally, we related interindividual variation in male agonistic behavior to variation in male weight. Our goal was to determine the factors that contribute to variation in the expression of social behavior in this species and to generate hypotheses related to behavior used in male–male competition.

## MATERIALS AND METHODS

### Maintenance and Care of Males

Males used in this study were reared from birth to last instar as family groups in plastic cages (27 × 20 × 10 cm) containing wood-shaving bedding, a paper tube shelter (11.5-cm length × 4-cm diameter), and ad libitum food and fresh water. Males were isolated at the last nymphal instar into individual cages (11 × 11 × 3 cm) containing food and water. This procedure ensured virginity and prevented males from learning about their competitive ability through interactions with other adult males. Controlling for social experience was necessary because our previous studies indicated that prior social interactions affected the expression and development of male agonistic behavior (Clark and Moore, unpublished data). Families can be reared together because nymphs do not display aggressive behavior. Males remained isolated until they were used in these experiments. Individuals were marked with a paper number glued to the pronotum for easy recognition. Prior to establishing social groups, males were weighed to within 0.0001 g using a Mettler balance (Model AE 100) on 2 consecutive days. We then used an average weight for each male in all analyses. All individuals were maintained in an environmentally controlled room under a 12:12 L:D photoperiod at 26–28°C.

### Establishment and Observation of Groups

We studied the agonistic interactions among male *G. portentosa* under two densities. Groups were composed of either five males (low density) or ten males (high density). The number of males representing a "low" or "high" density were selected arbitrarily. Just prior to the initiation of the scotophase on the first day of observation, unrelated males that were isolated at least 1 month and were of a similar age were placed together in glass arenas (51 × 25 × 30 cm) containing wood-shaving bedding, food, and water. These arenas also contained four wood platforms (10 × 5 × 1 cm) because earlier studies reported the use of platforms by socially dominant males (Nelson and Fraser, 1980). We established 10 low- and 10 high-density groups and scored the behavior of 148 males (two high-density groups contained only nine males due to deaths just prior to formation of groups). Once males were placed into a group, they remained together throughout the duration of the study.

Observations were conducted under a dim red light in an otherwise dark room. All social groups were housed in the observation room under a 12:12 L:D photoperiod at 26–28°C during the entire study. Observations were made during the scotophase. Social groups were observed a total of 14 days evenly spaced over 6 weeks. Each observation period consisted of 10–20 min of focal sampling of each group, which allowed us to observe the behavior of all males within the group. All behavioral acts for each individual were recorded during this observation period. Overall, each group was observed for an average 231 min (215–250 min).

We scored a total of 10 behaviors that are involved in social interactions among males (Table I). Abdomen Push, Butt, and Lunge have been shown to be associated with aggression, and Crouch and Retreat reflect submission (Nelson and Fraser, 1980; Breed *et al.*, 1981). We included Abdomen Flick among aggressive acts because it also involved contact between individuals. Abdominal Extension, Abdomen Thrash, Agonistic Hiss, and Stilt have been described (Nelson and Fraser, 1980; Breed *et al.*, 1981), however, because they do not involve contact between individuals, they have not been shown necessarily to reflect aggression. All behavior displayed by individual males was recorded and each behavior was expressed as the number of acts per minute observed.

## Statistical Procedures

Our first objective was to determine when rates of behavior within social groups became stable. We constructed a Pearson correlation matrix to determine if there was a significant correlation between rate of behavior displayed by individual males and each observation day. Because multiple comparisons were made on a single data set, the level of statistical significance was determined with Bonferroni-corrected probabilities (Rice, 1988). We also visualized the relationship between observation day and specific behavior using nonparametric regression. Nonparametric regression describes qualitative relationships between two variables of interest (Efron and Tibshirami, 1991). Nonparametric curves were generated using distance-weighted least-squares (DWLS) smoothing. This method produced a locally weighted curve through a set of points by least squares. Thus, the curve that was generated flexed locally and described deviations from linearity, resulting in a better fit to the data (Wilkinson, 1990). This technique therefore allowed us to estimate where inflection points occurred and determine the point at which behavioral rates stabilized. Once this date was determined, we constructed a second correlation matrix containing only those

**Table I.** Behavior Involved in Agonistic Interactions of Male *Gromphadorhina portentosa*

| Behavior | Description | Function |
|---|---|---|
| Abdomen Flick[a] | Thrust abdomen in an upward direction contacting opponent | Aggression |
| Abdomen Push[a] | Push another individual with the abdomen placed under the opponents body | Aggression |
| Abdomen Thrash[a] | Horizontal ahaking and beating of the abdomen on the substrate | Undescribed[b] |
| Abdominal Extension[a] | Extend and telescope the abdomen in an upward direction | Undescribed[b] |
| Agonistic Hiss[a] | Production of a distinct audible sound in the presence of other males | Undescribed[b] |
| Antenation | Contact with the antennae | Olfaction? |
| Approach | Directed movement toward another individual | Undescribed[c] |
| Butt[a] | Lower pronotum to expose horns and charge forward; contact made with horns | Aggression |
| Crouch[a] | Lower body against substrate and remain motionless | Submission |
| Lunge[a] | Forward thrust of the body toward an opponent | Aggression |
| Retreat[a] | Moving away from an individual and/or an interaction | Submission |
| Sideways-Lean | Drawing one side of the body toward the substrate | Undescribed[d] |
| Sit On | Sitting on or crawling over another individual | Undescribed[d] |
| Stilt[a] | Raising the front of the body off of the substrate | Undescribed[b] |

[a] Behavior addressed in this study.

[b] It has been documented that these behavioral acts occur during male–male interactions but they have not been shown to reflect aggression (Barth, 1968; Nelson and Fraser, 1980, Breed *et al.*, 1981; Leibensperger *et al.*, 1985).

[c] Approach may be aggressive if it results in the display of subordinate behavior by an opponent (Breed *et al.*, 1981).

[d] Breed *et al.* (1981) describe "sit on" and "sideways-lean." Neither of these was assigned a function by these researchers.

observations after the date behavior stabilized. Previously significant correlations should then be nonsignificant if behavior is indeed stable after this point. Statistical significance was again determined by Bonferroni-corrected probability.

We also examined the influence of the social environment on the rate of behavior displayed by individual males within stable social groups. We did not include males that displayed only subordinate behavior or no behavior ($N = 17$ of 98 for high density; $N = 5$ of 50 for low density) in our analyses because we were interested in quantifying variation among males in the display of aggressive behavior. Because groups were formed by arbitrarily placing unrelated individuals together, we had no a priori expectation that each social group would have a similar composition. Therefore, to control for potential variation resulting from special characteristics of each group of males, we used a nested analysis of variance (groups within densities) to determine the effect of male density on the rate of various agonistic behaviors displayed while controlling for group effects (Sokal and Rohlf, 1981, pp. 272). Behavioral rates were ranked prior to analysis because we could not meet the assumption of normality for a parametric analysis of variance (Kramer and Schmidhammer, 1992).

To describe variation in aggression among all males, we used a principal-components analysis (PCA) to reduce a subset of our data (Abdomen Flick, Abdomen Push, Butt, Lunge) expected a priori to be correlated. This subset of behavior was chosen because each behavior was known to reflect aggression and involved contact between interactants. The PCA generated three new and uncorrelated variables related to aggression. We then examined the relationship between our new measures of aggression and behavior that had not been assigned a function or had not been previously shown to be associated with aggression. We constructed a Pearson correlation matrix between male aggression and rate of Abdominal Extension, Abdomen Thrash, Agonistic Hiss, and Stilt with significance determined by Bonferroni-corrected probabilities.

Finally, we examined the relationship between male weight and interindividual variation in aggression and other agonistic behavior with a Pearson correlation matrix. Significant correlations were determined with Bonferroni-corrected probabilities. Male weights were log transformed prior to analysis to meet assumptions of normality. Nonparametric relationships between behavior and weight were visualized using the nonparametric regression technique described above.

We analyzed all data using the SYSTAT statistical package (Wilkinson, 1990).

## RESULTS

### Diversity of Behavior

Overall, the behavior seen in groups of males was the same as that described for pairs of males. We observed the same diversity of behavior as described by Nelson and Fraser (1980) and Breed *et al.* (1981). We have standardized terms where they differed among studies. Barth (1968) noted that winners of social interactions sometimes slapped their abdomens against the opponent as well as on the substrate. Breed *et al.* (1981) referred to this behavior as Abdominal Wiggle, and Nelson and Fraser (1980) termed this Abdomen Thrash. While they apparently considered this one behavior, we separated it into two distinct acts. We referred to the horizontal shaking and beating of the abdomen on the substrate as Abdomen Thrash, while Abdomen Flick referred to a male slapping his abdomen against another male. We also considered Abdomen Flick to be aggressive because contact was made with the opponent. We used the term Abdomen Push in place of Abdomen Thrust (Breed *et al.*, 1981) to avoid confusion with the term Abdomen Thrash. Consistent with Breed *et al.* (1981), we described the expansion and extension of the abdomen as Abdominal Extension, whereas Nelson and Fraser (1980) terms this behavior Posturing. Breed *et al.* (1981) described the two behaviors that we termed Butt and Lunge as a single behavior, Ram. We made this distinction because Butt involved a forward movement that resulted in contact with the opponent. Lunge involved a forward movement directed toward another individual, however, contact was not made. Nelson and Fraser (1980) reported that males occasionally bit their opponent on the back, legs, or antennae. We noted no clear instances of biting during this study or in subsequent observations (Clark and Moore, unpublished data). Breed *et al.* (1981) also described Sideways Leaning, which involved drawing one side of the body toward the substrate. Breed *et al.* (1981) did not ascribe a function to this behavior. We saw no instances of Sideways Leaning in our groups, although we have observed Sideways Leaning during subsequent experiments where we observed dyads. Individuals appear to lean toward an approaching opponent, indicating a possible defensive role. It is, at best, an infrequently performed act (Breed *et al.*, 1981).

### Stability of Behavior

The rates of some acts changed over the observation period (Table II). The rate of Butt was significantly correlated ($r = 0.084$, $N = 2036$, $P < 0.001$, Bonferroni significance = 0.005) with observation day (the length of time in days between formation and observation day). The rates of Abdomen Thrash ($r = 0.043$, $N = 2036$, $P = 0.052$) and Agonistic Hiss ($r = 0;043$, $N = 2036$, and $P = 0.051$) were not significantly correlated with day of observation at a Bonferroni-corrected level of significance (Bonferroni significance = 0.0056) but did show a weak association. None of the correlations between observation day and Abdomen Flick, Abdomen Push, Abdominal Extension, Lunge, Stilt, Crouch, and Retreat were significant (all $P$'s > 0.116). Nonparametric regression (data not shown) indicated a common inflection point for all three acts that increased during early interactions. The rate of these three acts increased slightly during the first five observation periods (1–10 days after group formation) but were stable for the rest of the study (10–37 days after group formation). Because the increased rates occurred in acts that were of interest, we eliminated observations that occurred during early stages of interactions. A second Pearson correlation matrix using only those observations that occurred after day 10 indicated no significant correlations between observation day and rate of any behavior (all $P$'s > 0.350) except Retreat ($r = 0.056$, $N = 81$, $P = 0.044$). However, rate of Retreat was not significantly correlated with observation day at a Bonferroni-corrected level of significance ($P = 0.005$). Furthermore, because this study was concerned mainly with aggressive, or potentially aggressive acts, we

**Table II.** Mean Rates of Behavior (±SE) for Males Observed at Two Densities

| Behavior | No. of acts/min<br>Low density<br>($N = 45$ males) | <br>High density<br>($N = 81$ males) | Effect of density[a]<br>(df = 1,106) | Among-group difference<br>(df = 18,106)[a] |
|---|---|---|---|---|
| Abdomen Flick | 0.0037 ± 0.0012 | 0.0056 ± 0.0012 | $F = 0.206$, $P = 0.651$ | $F = 2.704$, $P = \mathbf{0.001}$ |
| Abdomen Push | 0.0036 ± 0.0014 | 0.0147 ± 0.0029 | $F = 10.787$, $P = \mathbf{0.001}$ | $F = 5.009$, $P < \mathbf{0.001}$ |
| Butt | 0.0309 ± 0.0070 | 0.0377 ± 0.0053 | $F = 2.436$, $P = 0.122$ | $F = 1.255$, $P = 0.233$ |
| Lunge | 0.0056 ± 0.0016 | 0.0055 ± 0.0012 | $F = 0.500$, $P = 0.824$ | $F = 0.515$, $P = 0.946$ |
| Abdominal Extension | 0.0155 ± 0.0046 | 0.0099 ± 0.0015 | $F = 0.146$, $P = 0.703$ | $F = 0.615$, $P = 0.881$ |
| Abdomen Thrash | 0.0315 ± 0.0078 | 0.0251 ± 0.0037 | $F = 1.036$, $P = 0.311$ | $F = 1.479$, $P = 0.112$ |
| Agonistic Hiss | 0.0957 ± 0.0217 | 0.1135 ± 0.0194 | $F = 0.421$, $P = 0.518$ | $F = 1.967$, $P = \mathbf{0.018}$ |
| Stilt | 0.0109 ± 0.0024 | 0.0162 ± 0.0030 | $F = 0.890$, $P = 0.348$ | $F = 3.344$, $P < \mathbf{0.001}$ |
| Crouch | 0.0018 ± 0.0007 | 0.0016 ± 0.0005 | $F = 0.017$, $P = 0.895$ | $F = 0.939$, $P = 0.534$ |
| Retreat | 0.0162 ± 0.0040 | 0.0145 ± 0.0021 | $F = 0.211$, $P = 0.647$ | $F = 2.082$, $P = \mathbf{0.011}$ |

[a] From a nested analysis of variance with among-group differences nested under the two density treatments.

made no further correction for this trend. In addition, nonparametric regression of each behavior and observation after day 10 indicated that rate of aggressive or potentially aggressive behavior during this period was stable as well as uncorrelated. Therefore, all subsequent analyses were performed on the overall rate of behavior occurring during this stable period.

## The Effect of Density

The nested analysis of variance indicated that there were significant differences among groups in the expression of the aggressive behaviors Abdomen Flick ($F = 2.704$, df = 18,106, $P = 0.001$) and Abdomen Push ($F = 5.009$, df = 18,106, $P < 0.001$), as well as Agonistic Hiss ($F = 1.967$, df = 18,106, $P = 0.018$), Retreat ($F = 2.082$, df = 18,106, $P = 0.011$), and Stilt ($F = 3.344$, df = 18,106, $P < 0.001$). There were no significant differences among groups in any of the remaining acts (all $P$'s $> 0.112$).

The behavioral rates of males within different density treatments varied (Table II). In the high-density treatment, males displayed Abdomen Push more often than males in the low-density groups ($F = 10.787$, df = 1,106, $P = 0.001$). The rates of the remaining acts were less affected by male density. However, regardless of density, all of the behaviors defined in Table I occurred in all groups.

Although only the rate of Abdomen Push was affected by density, we analyzed data from the high and low densities separately in all subsequent analyses. The trends in significant and nonsignificant results were the same at both densities. Our conclusions based on separate analyses were therefore the same regardless of density. For the sake of brevity we present data only from the high-density treatment.

## Variation in Male Behavior

Not all males interacted or interacted infrequently during our observations. Therefore, we did not attempt to define the structure of male social groups based on this study. Males did, however, vary in aggression. We used principal-components analysis to provide aggregate measures of overall aggression (Table III). The first three principal-component scores together accounted for 94.5% of the observed variation in male aggressive behavior. Principal component 1 (PC1) accounted for over half of the total variation. All of the behaviors had strong and positive loadings on this component. Thus, the first component was a measure of aggression and was used as an Aggression Index. The second variable (PC2) contrasted Butt and Lunge with Abdomen Flick and Abdomen Push (Table III). Given the nature of the behavior contrasted, this component apparently distinguished frontal assaults from assaults involving the abdomen. The relationship between the Aggression Index (PC1) and PC2 suggested that

Table III. Principal-Components Analysis of Aggressive Behavior

| | Component loading | | |
|---|---|---|---|
| | PC1 | PC2 | PC3 |
| Abdomen Flick | 0.532 | 0.724 | 0.439 |
| Abdomen Push | 0.662 | 0.353 | −0.661 |
| Butt | 0.873 | −0.337 | 0.106 |
| Lunge | 0.856 | −0.379 | 0.130 |
| Eigenvalue | 2.218 | 0.905 | 0.648 |
| Percentage total variance explained | 55.44 | 22.63 | 16.45 |

more aggressive males utilized frontal assaults during interactions, while males displaying lower levels of aggression preferentially used the abdomen during agonistic interactions (Fig. 1a). Thus, Butt and Lunge appeared to be highly aggressive. Only Abdomen Flick and Abdomen Push had strong loadings on our third principal component (PC3). PC3 contrasted the positively loading Abdomen Flick with the negatively loading Abdomen Push. The relationship between the Aggression Index and PC3 visualized by nonparametric regression indicated that Abdomen Flick was a slightly more aggressive behavior than Abdomen Push (Fig. 1b).

The use of PC1 as an Aggression Index allowed us to examine potential relationships between aggression and other noncontact behavior occurring during male–male interactions. We found that the Aggression Index was significantly correlated with Abdominal Extension ($r = 0.222$, $N = 81$, $P = 0.047$), Abdomen Thrash ($r = 0.699$, $N = 81$, $P < 0.001$), Agonistic Hiss ($r = 0.436$, $N = 81$, $P < 0.001$), and Stilt ($r = 0.555$, $N = 81$, $P < 0.001$). Nonparametric curves indicated that the relationship between the Aggression Index and three of these variables was positive and nearly linear, while the relationship between the Aggression Index and Abdominal Extension was slightly curvilinear (Figs. 2a–d). Despite this nonlinearity, the rate of Abdominal Extension still increased with increasing values of the Aggression Index (Fig. 2a). Abdominal Extension ($r = -0.241$, $N = 81$, $P = 0.030$), Abdomen Thrash ($r = -0.161$, $N = 81$, $P = 0.152$), and Agonistic Hiss ($r = 0.181$, $N = 81$, $P = 0.106$) were negatively correlated with submissive behavior (Retreat and Crouch). While these correlations were in the expected direction, they were not significant (Bonferroni significance level $P = 0.0125$). Stilt was positively, although not significantly, correlated with submissive behavior ($r = 0.240$, $N = 81$, $P = 0.031$).

## The Effect of Male Weight

One common explanation for variation among males in aggression is a correlation between size and fighting. We found no strong association between

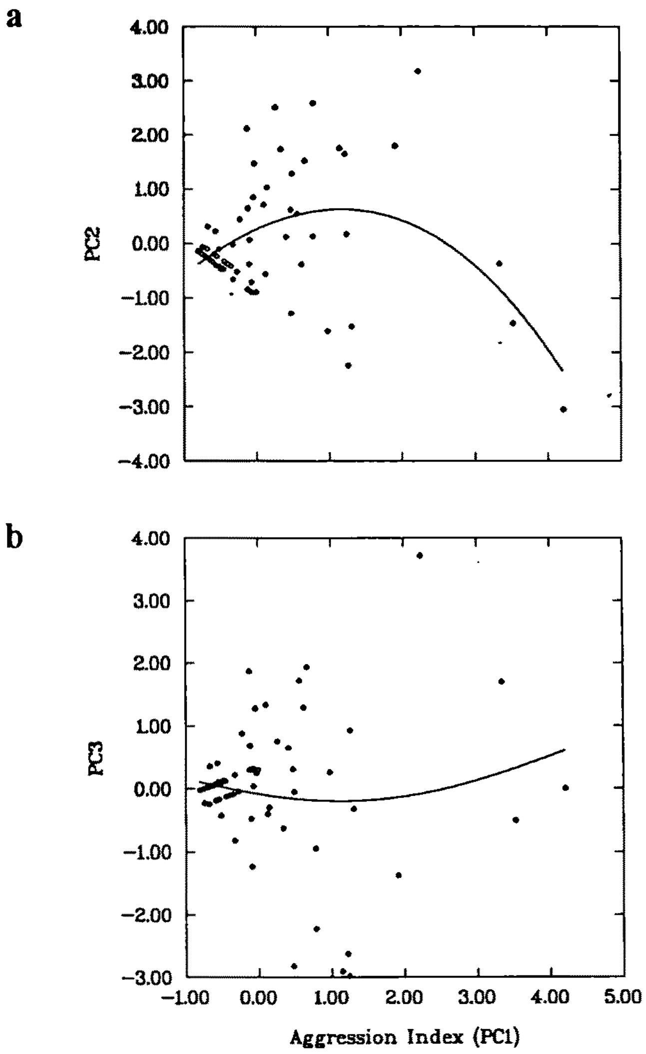

**Fig. 1.** Relationship between (a) the Aggression Index (PC1) and PC2 and (b) the Aggression Index and PC3. The regression line was generated using DWLS nonparametric regression (Wilkinson, 1990). PC2 contrasted the negatively loading Butt and Lunge with the positively loading Abdomen Flick and Abdomen Push (a). PC3 contrasted the positively loading Abdomen Flick with the negatively loading Abdomen Push (b).

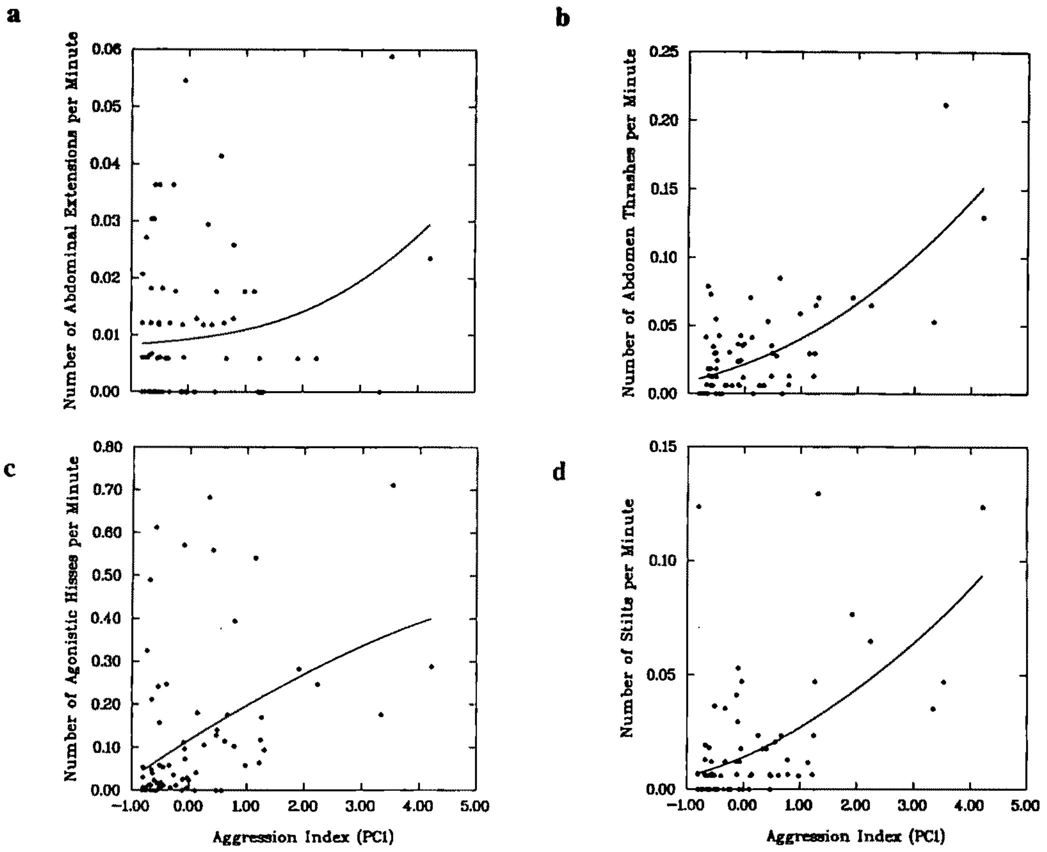

**Fig. 2.** Nonparametric curves reflecting the relationship between the Aggression Index and behavior with previously undetermined function. The Aggression Index was primarily linearily related and significantly correlated with Abdominal Extension (a; $P = 0.047$), Abdomen Thrash (b; $P < 0.001$), Agonistic Hiss (c; $P < 0.001$), and Stilt (d; $P < 0.001$).

male weight and aggression. The strongest relationship observed was between male weight and Abdominal Extension; however, this correlation was not statistically significant ($r = 0.213$, $N = 81$, $P = 0.056$). Male weight was not significantly correlated with Abdomen Flick ($r = 0.129$, $N = 81$, $P = 0.250$), Abdomen Push ($r = 0.143$, $N = 81$, $P = 0.203$), Butt ($r = -0.004$, $N = 81$, $P = 0.969$), Lunge ($r = 0.049$, $N = 81$, $P = 0.667$), Abdomen Thrash ($r = -0.026$, $N = 81$, $P = 0.817$), Agonistic Hiss ($r = 0.085$, $N = 81$, $P = 0.450$), or Stilt ($r = 0.070$, $N = 81$, $P = 0.537$). There was no correlation between male weight and the Aggression Index (PC1, $r = 0.091$, $N = 81$, $P = 0.421$), PC2 ($r = 0.140$, $N = 81$, $P = 0.211$), or PC3 ($r = -0.048$, $N = 81$, $P = 0.667$).

Although the linear relationship between male weight and behavior was, at best, weak, there were interesting trends. Reflecting the overall lack of significance, aggression increased only slightly with increasing weight. However, bigger males were more likely to use their abdomen in contests and bigger males used Abdomen Push more than Abdomen Flick. Among the behavior with unknown function, the rate of Abdominal Extension also increased with male weight. However, the highest expression of Abdomen Thrash, Agonistic Hiss, and Stilt was at the midweight.

## DISCUSSION

Our focus on the behavior of males in groups rather than pairs provides additional insights and generates hypotheses concerning the influence and role of male–male competition in *G. portentosa*. We found that the rate of one aggressive behavior in groups increased over time before stabilizing. This is contrary to the expected prediction that aggression and overt fighting would decrease as individuals established stable associations (Kaufmann, 1983). Males at high densities were expected to show higher levels of aggression, yet we found that only Abdomen Push was influenced by density. As expected, Abdominal Extension, Abdomen Thrash, and Agonistic Hiss reflected aggression in our study. However, not all of the behavioral acts we examined were found to be aggressive. Stilt was positively correlated with submission and aggression. Therefore, its function, if any, in agonistic encounters is still unknown. Finally, contrary to expectation and the previous suggestion of Barth (1968), we found that male weight had little effect on behavior.

*G. portentosa* males utilize a number of aggressive, submissive, and stereotyped acts during male–male interactions. The rate of aggressive behavior increased initially but stabilized as predicted for the establishment of stable social associations. Once stable, aggressive interactions continued at this increased, but constant, rate over a long period. Increased levels of aggression after the establishment of stable associations have been described in other cockroaches [e.g., *Nauphoeta cinerea* (Moore *et al.*, 1988)]. These results suggest that social interactions between *G. portentosa* males are highly structured. However, in this study as in all of the previous studies of *G. portentosa*, the overall rates of interactions were relatively low. There is considerable variation among males in the level of aggressive behavior displayed.

We observed the same diversity of agonistic behavior in low-density and high-density groups as Nelson and Fraser (1980) and Breed *et al.* (1981) described for pairs of males. Male density had little effect on the rates of behavior displayed by individual males. Abdomen Push was the only behavioral rate that was significantly influenced by density in our study. In other insects higher densities result in increased interactions (Ewing, 1972; Borgia, 1981; Moore, 1987; Gautier *et al.*, 1988). However, there are examples where density was found to have no effect (Breed and Byers, 1979). The lack of a density effect for *G. portentosa* suggests that the social system of this species is less well developed despite the complex behavioral repertoire that occurs during social interactions. Therefore, like *Byrsotria fumigata* (Breed and Byers, 1979), while interactions are structured, it is less clear that this results in a structured social system.

This study also suggests some potential hypotheses for the function of male *G. portentosa* behavior in groups. By using PCA to reduce the set of behavior known to be associated with aggression (Abdomen Flick, Abdomen Push, Butt, Lunge), we generated both a description of aggression and an Aggression Index. We found that more aggressive males utilized frontal assaults (Butt, Lunge) during interactions, while males displaying lower levels of aggression preferentially used the abdomen during interactions. These results suggest that Butt and Lunge are highly aggressive behaviors that play an important role in agonistic contests. The PCA also indicated that more aggressive males performed Abdomen Flick more frequently, while males displaying lower levels of aggression preferentially used Abdomen Push.

Our suggestions are consistent with those of Breed *et al.* (1981), who found that Ram, a behavior that we separate into Butt and Lunge, was a highly aggressive behavior (see also Barth, 1968; Nelson and Fraser, 1980). Overall, the PCA suggests that, in addition to varying in the expression of behavior, males also vary in the specific aggressive behaviors they employ during aggressive interactions. We suggest that Butt and Lunge are the most aggressive behaviors, while Abdomen Flick and Abdomen Push, although frequently performed, are less aggressive and more ritualized behaviors.

We also investigated behavior that was described previously but was not associated with aggression. We found that Abdominal Extension, Abdomen Thrash, and Agonistic Hiss were positively correlated with our aggregate measure of male aggression. The rate of expression for each of these behavioral acts increased with increasing aggression. Abdominal Extension, Abdomen Thrash, and Agonistic Hiss were also negatively correlated with submissive behavior. Because these behaviors are often performed with some distance between individuals, and therefore do not involve contact, their relationship to aggression suggests the intriguing possibility of functioning as status cues or displays. Stilt was positively correlated with both aggressive and submissive behavior. This relationship indicates that Stilt is neither aggressive nor subordinate, therefore its function in male–male interactions remains unknown.

One mechanism giving rise to social associations in a group is the assessment of fighting ability from physical attributes, such as body size (Thornhill, 1983; Hoffman, 1988; Boake, 1989; Faber and Baylis, 1993), or behavioral attributes, such as aggression (Maynard Smith, 1982; Kaufmann, 1983). Our results suggest that *G. portentosa* uses noncontact behaviors as displays, but it is not clear what is being signalled. There is no obvious relationship between male size and behavior. None of the behaviors were significantly correlated with weight. The highest expression of Abdomen Thrash, Agonistic Hiss, and Stilt was at the midweight. Only Abdominal Extension increases with increasing male weight. There is an increasing relationship between Abdomen Thrash, Abdominal Extension, Agonistic Hiss, and aggression (Fig. 2), so it may be that displays are used to signal potential levels of aggression by individuals. Further experiments will be needed to test these hypotheses.

Male–male interactions among male *G. portentosa* include overt aggression (Barth, 1968; Nelson and Fraser, 1980; Breed *et al.*, 1981), aggressive displays (this study), acoustic signals (Nelson, 1979), and perhaps olfactory signals (Nelson and Fraser, 1980). The method *G. portentosa* uses to produce acoustic signals is unusual for an insect. Further, the use of such complicated acoustical signals during social competition in a cockroach is rare (Roth and Hartman, 1967). The use of diverse behavior and signals in ritualized fights and displays suggests that social interactions are important in this species. However, although social behavior is well developed, the structure of the social group in this species is less clear. Males do form associations that appear to reflect differences in rank (Leibensperger *et al.*, 1985). Social status may have fitness consequences for male *G. portentosa*; females discriminate among males differing in rank, presumably on the basis of pheromonal cues (Leibensperger *et al.*, 1985). Still it is not clear that territoriality, or a dominance hierarchy, occurs. Thus, while the behavioral repertoire of this species is now well described, future studies will be needed to understand the consequence, and perhaps the evolution, of the diverse and complex behavior structuring social interactions in *G. portentosa*.

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