

A behavioral syndrome linking courtship behavior toward males and females predicts reproductive success from a single mating in the hissing cockroach, *Gromphadorhina portentosa*

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Suites of correlated behaviors, or “behavioral syndromes,” have been shown to occur throughout the animal kingdom. Behavioral syndromes involving sexual selection are expected to have significant evolutionary ramifications, but few studies have linked behavioral syndromes to sexual selection. We measured the behavior of male hissing cockroaches (*Gromphadorhina portentosa*) during male–male competition, female choice, and 3 other ecologically relevant contexts and quantified between-context correlations in behavior. We found that aggression directed toward an opponent and retreat and courtship elicited from an opponent were repeatable among males, suggesting that individuals exhibit stable behavioral types in the context of male–male interaction. Our analyses also revealed a “fast–slow” syndrome, linking behavior in a self-righting context to behavior in a foraging context. In contrast to data from several other species, fast–slow scores in hissing cockroaches were not correlated with aggression in a male–male context. Finally, we identified a new type of behavioral syndrome, which we call “libido.” Libido was defined by a positive relationship between courtship directed toward opponents in a male–male context and courtship directed toward potential mating partners in a male–female context. Among males that copulated, libido scores predicted reproductive success. We conclude that the libido syndrome, coupled with sexual selection favoring high courtship intensity in a male–female context, may be responsible for the persistence of male–male courtship behavior in this population. *Key words:* animal personalities, behavioral spillover, false discovery rate, homosexual behavior in animals, order effects, pseudofemale behavior. [*Behav Ecol* 20:781–788 (2009)]

A number of empirical studies on phylogenetically diverse taxa, including arthropods (e.g., Johnson and Sih 2005), cephalopods (e.g., Sinn et al. 2008), and vertebrates (e.g., Bell 2005; Dingemanse and Reale 2005), indicate that individuals in a population differ with respect to their behavioral tendencies and that an individual’s behavior in a given context can predict its behavior in other contexts (reviewed in Sih, Bell, and Johnson 2004; Sih, Bell, Johnson, and Ziemba 2004; Bell 2007). Reconciling behavioral ecological models of optimal behavior with the reality of individual differences and interdependent patterns of behavior requires an improved understanding of individual differences, the contexts in which behaviors covary, and the fitness trade-offs mediating behavior across contexts (Sih, Bell, Johnson, and Ziemba 2004).

In the present study, we examined 2 related phenomena: repeatability of behavior and between-context “behavioral syndromes.” Repeatability of behavior is demonstrated by positively correlated behavior scores between 2 or more sets of observations on the same individuals in the same behavioral context. For example, an individual might consistently behave more aggressively than the population average when confronting a conspecific. Less obviously, an individual might consistently elicit certain types of behavior from other individuals with whom it interacts. We call the latter phenomenon, “repeatability of elicited behavior.”

A “behavioral syndrome is a suite of correlated behaviors across multiple (2 or more) observations” (Sih, Bell, Johnson,

and Ziemba 2004, p. 246). In this study, we test for between-context behavioral syndromes, defined as suites of correlated behaviors occurring in more than one context (where “context” refers to a broad behavioral category such as territory defense or foraging; Sih, Bell, and Johnson 2004; Sih, Bell, Johnson, and Ziemba 2004). An axis describing covariation in 2 or more behavioral contexts functionally defines a behavioral syndrome. An individual’s location on such an axis represents its behavioral type (BT) with respect to that syndrome.

The definition of behavioral syndrome does not require the demonstration of repeatability for the constituent behaviors (Sih, Bell, Johnson, and Ziemba 2004; Sih and Bell 2008), and several previous reports describe behavioral syndromes without explicitly demonstrating repeatability (e.g., Bell and Sih 2007; Dochtermann and Jenkins 2007; Kortet and Hedrick 2007; Moretz et al. 2007). Importantly, however, the demonstration of between-context behavioral syndromes does imply continuity in behavioral tendencies, if not repeatability per se. Under the null hypothesis that there are no enduring behavioral differences between individuals (i.e., that individuals are randomly assigned behavioral tendencies between observations in contexts A and B), we would not expect significant positive correlations between behaviors in contexts A and B. Thus, the observation of significant correlations between contexts implies underlying consistency in behavioral tendencies given the caveat that the experimental design controls for order effects. Failure to control for order effects could give rise to spurious syndromes (syndromes that do not reflect preexisting differences among individuals) if factors experienced in one context influence the animal’s behavior in a later context (see Order effects in Methods).

Although Behavioral Syndromes theory suggests that correlations between behavioral traits should have strong effects on

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the operation of natural selection, there exists remarkably little data on the fitness consequences of behavioral syndromes (Sih, Bell, Johnson, and Ziemba 2004; Smith and Blumstein 2008). The authors of a recent meta-analysis on the effects of personality on fitness (Smith and Blumstein 2008) were able to identify only one study that related a behavioral syndrome to a measure of fitness (but see van Oers et al. 2008). The study they point to showed that mating “activity” in a group of water striders (*Aquarius remigis*) depended on the activity level of the males in the group, where activity was a composite measure of behavior across contexts taken prior to the mating trials (Sih and Watters 2005). This is an intriguing finding because it suggests that behavioral syndromes affect the operation of sexual selection (see also Stapley and Keogh 2005). Further research is needed to determine whether and how behavioral syndromes affect sexual selection in other taxa. Of particular interest are the specific relationships among behaviors in the contexts of male–male competition and female choice and the relationships between behavior in those contexts and behavior in other contexts that are not directly involved in sexual selection. Identifying these relationships opens the door to elucidating the fitness-related ramifications of BT with respect to sexual selection.

We investigated sexual selection and behavioral syndromes in a laboratory colony of Madagascar giant hissing cockroaches (*Gromphadorhina portentosa*, “hissing cockroaches” hereafter). Hissing cockroaches offer several advantages for behavioral syndromes research: they thrive in the laboratory, exhibit a wide range of easily observed behaviors, and are highly social (but not eusocial). Social animals are particularly interesting subjects for behavioral syndromes research because social roles may vary as a function of BT (e.g., proactive producers, reactive scroungers) and group properties may depend on the mix of BTs in the group (Sih and Watters 2005).

For the present study, we identified how behavior during male–male competition and female choice are linked to behavior in other contexts. Specifically, we quantified males’ behavior in a territory intrusion context, a courtship context, and 3 ecologically relevant contexts that were not directly related to sexual selection (self-righting, disturbance, and foraging). We then identified behavioral syndromes linking behavior across contexts and related males’ BTs to their reproductive success during the courtship assay. The goals of our study were to describe repeatability of behavior and behavioral syndromes in male hissing cockroaches and to test the hypothesis that male–male competition, female choice, or both processes are correlated with behaviors in other contexts.

METHODS

Study animals

Females and focal males were drawn from a breeding colony originally purchased from VWM Reptiles (Edinburg, IL). Opponents for the “intruder” assays (see below) were adults derived from a separate colony, originally purchased from New York Worms (Long Island, NY). Females and focal males were removed from the breeding colony and placed in same-sex juvenile colonies once they exhibited sexually dimorphic subgenital plates (the third or fourth instar). 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”, China) to measure the maximum length and maximum width of the pronotum. Large, freshly molted females were deemed “putative adults” and housed with other putative adult females that molted on the same day. We could not be certain that these

females were actually adults, so we marked them with correction fluid and checked them daily to determine if they molted again. All animals had access to cardboard egg crate shelters, an ad libitum supply of Purina Dog Chow (Nestlé Purina Pet-Care Company, St Louis, MO) and water, and weekly supplements of apples and carrots. Animals were maintained in a 12:12 h reversed light:dark cycle, at 28 °C, and 50% humidity.

Behavioral assays

Each of 70 focal males was subjected to 5 randomly ordered assays. In 3 of the assays (righting, saline, and foraging), we observed animals’ behavior in an asocial, potentially stressful situation. In the other 2 assays (intruder and female), we observed their behavior in social interactions. We conducted the first assay 14 days after the focal male’s final molt. Males were subjected to subsequent assays at 7 day intervals. Experiments took place in a heated room (28 °C) that was separate from the animal housing area. All assays began with a 5-min acclimation period in the testing room. We weighed the males after each trial.

Righting assay

The “righting” assay tested latency to move under stress and righting agility in an ecologically relevant context (males are often flipped onto their backs during conflicts with other males). This assay is similar to “tonic immobility” tests that have contributed to a number of studies on personality in animals (e.g., Jones et al. 1995; Erhard et al. 1999). Righting trials were conducted with the lights on and video recorded from above (Sony Handicam DVD103, Sony Electronics Inc., San Diego, CA). Males were placed on a glass plate, which had been coated with water-based lubricating jelly (Health Care Plus, Canadian Custom Packaging, Toronto, ON). The experimenter inverted the glass plate and gently pinned the animal against a veneer table top. After 3 s, the glass was rapidly lifted, leaving the male ventral side up on the table. Typically, the male froze for a moment and then twisted his abdomen and moved his legs to right himself. The assay was immediately repeated 2 more times. Video recordings were later analyzed frame by frame to determine the times at which 1) the glass was removed, 2) the male first flexed his abdomen toward the substrate, and 3) at least 5 of the male’s legs were supporting his weight. Averaging over all 3 trials, the interval (2–1) defined the variable “latency to move” and the interval (3–2) defined the variable “latency to right.” Separating these 2 measures was suggested by previous work in rats (*Rattus norvegicus*; Pellis et al. 1991).

Saline assay

The “saline” assay tested reactivity to a startling stimulus. Hissing cockroaches emit loud hisses when disturbed (Nelson and Fraser 1979). A pilot study showed that applying salt water to the dorsum was an easily standardized method of eliciting this disturbance response. With the lights on, the experimenter used a water dropper to apply 3 drops (~1 drop/s) of saline solution (0.25 M) from a height of 10 cm. Drops were aimed at the dorsal junction of the thorax and abdomen. The experimenter recorded the number of hisses emitted by the animal in 60 s.

Foraging assay

The “foraging” assay tested the animals’ latency to emerge from a shelter to forage on a novel food item. Males were deprived of food for 48 h prior to testing. Room lights were

turned off, and video recordings were made under near infrared (NIR) illumination. After removing all objects from the male's enclosure, the experimenter placed the male under a weighted opaque plastic cup (10 cm diameter \times 5 cm high) at one end of his enclosure. The interior of the cup was coated with petroleum jelly and mineral oil to prevent climbing. A door (2 cm high \times 6 cm wide) on one side of the cup could be removed and reattached with hook-and-loop fabric. One gram of previously frozen, ripe banana (a novel food for these individuals) was placed on a food dish 5 cm from the front of the plastic cup. *Gromphadorhina portentosa* are highly motivated to eat bananas (Logue DM, unpublished data). After the 5-min acclimation period, the experimenter removed the door of the cup. We defined the time it took for the male's head to cross the plane of the door as the latency to emerge, and the time that it took the male to begin eating as the latency to eat. If the male did not eat within 1800 s, the trial was terminated and values of 1800 s were entered for the 2 variables.

Intruder assay

The "intruder" assay was used to measure behavior in the presence of a male intruder in the focal male's cage. Water tubes and shelters were removed from the male's enclosure, and the sides of the enclosure were coated with a mixture of petroleum jelly and mineral oil to prevent escape. Intruder trials were conducted in the dark and recorded from above with NIR video. We used the metric pronotum width \times pronotum length to size match focal males to opponents. Each focal male was subjected to exactly one intruder trial, but some opponent males (17 of the 25 opponents) were used in multiple trials to facilitate size matching (as in Bell and Stamps 2004; average \pm standard deviation = 3.04 ± 1.97 trials/opponent). After the acclimation period, the experimenter introduced the opponent into the focal male's enclosure, such that the 2 males touched antennae. Trials lasted for 15 min, and both males were weighed after the trial. Observers scored trial videos for the following behaviors from each male: abdomen flick (abdomen moves laterally to strike), butt (posterior-anterior strike with the pronotum), flip opponent (scored when an abdomen flick or butt causes the target animal to land on its dorsum), chase, thrash (lateral thrashing of the abdomen against the substrate, each cycle is counted as one thrash), approach, latency to butt, latency to thrash, withdraw, climb walls, hiss, and thrust (anterior-posterior movement of the abdomen; measures adapted from Nelson and Fraser 1979; Breed et al. 1981; Clark and Moore 1995).

Female assay

The "female" assay was used to measure behavior in the presence of a virgin female. Preparation and recording were the same as in the intruder assay. A virgin female (14–29 days after her adult molt) was introduced into the male's enclosure, and the 2 animals were made to touch antennae. Individual females were never used in more than one trial. Trials lasted for 30 min, and both individuals were weighed after the trial. Observers scored videos for the following behaviors from the males: thrust, hiss, latency to hiss, latency to thrust, thrash, approach, and withdraw. Because copulation is exclusive to other behaviors, all variables except latencies were divided by the time to copulate (or by 1800 s if the pair did not copulate) to produce rates of behavior. Females that did not copulate were housed individually after being used in a trial. If they died within a week or molted within 2 months, the data from their trial were thrown out, and the male with whom they interacted was subjected to another female assay ($N = 6$). Otherwise, focal males were never subjected to more than one female assay.

Females that copulated were maintained in isolation in a plastic container (21.5 cm long \times 14.5 cm wide \times 4.5 cm high) with ad libitum access to dog chow, carrots, and water until giving birth (*G. portentosa* bear live young) or 180 days (median gestation = 73 days, maximum observed = 155 days).

Data scoring

Observers scored the data "blindly" with respect to the subject's performance in other tests. Data within each assay were scored by one observer (female, saline, foraging) or 2 observers (intruder, righting) who trained together until they achieved high interobserver reliability (we did not quantify interobserver reliability). Four video recordings were corrupted, resulting in sample sizes of 69 intruder trials and 67 righting trials.

Notes on behavior

Some intruder trials were characterized by little or no activity, others by intense fighting, and still others by male–male courtship behavior including courtship hissing and thrusting. Male–male courtship (as evidenced by at least one thrust from either the focal male or the opponent) was observed in 20% of intruder trials.

In 6% of female trials, the male pushed the female into a corner and appeared to gain intromission by force. After this happened, the female typically walked in wide circles, vigorously twisting her abdomen, and kicking the male with her hind legs, until he withdrew. These apparently forced copulations were much briefer than normal copulations, never resulted in offspring, and were usually followed by additional courtship from the male, so we did not count them as "successful matings" in the final data set.

Data reduction

Data were visualized as histograms, and right-skewed variables were log transformed. We then conducted within-assay principal components analyses (PCAs) for foraging, intruder, and female assays. Data from saline assays included only one variable (number of hisses), and so these could not be reduced by PCA. Data from righting assays included 2 variables (latency to move and latency to right), but these variables were not correlated, so reduction with PCA would have been inappropriate.

Within-context repeatability

Some of the opponents in the intruder assay were tested multiple times, allowing us to measure the repeatability of their behavior. We used Pearson's correlation with 10 000 randomizations to determine whether an opponent's behavior in its first trial predicted its behavior in its second trial. For the purpose of these tests, the between-trial variation in the opponent males' behavior that is attributable to the focal males' interindividual variation in behavior contributes to Type II (conservative) error. Repeatability is manifested by a positive correlation. It was appropriate to use 1-tailed significance tests here because we were not testing for deviance generally from a random association between the variables but were specifically testing whether the data were more positively associated than would be expected by chance. We were also interested in whether individual opponents consistently elicited certain patterns of behavior from the focal males, so we used the same technique to compare the focal male's behavior during a given opponent's first trial versus the (different) focal male's behavior during that opponent's second trial.

Each focal male was subjected to 3 righting trials in rapid succession. Thus, we were able to quantify repeatability in this context, but we point out that any uncontrolled factors that covary with time (e.g., activity phase) would be confounded with individual identity, potentially inflating measure of repeatability. We used Pearson's correlation with 10 000 randomizations to compare log transformed latencies to move and to right in trials 1 versus 2, 2 versus 3, and 1 versus 3.

Behavioral syndromes

For the present study, we looked for between-context correlations in a large set of behaviors that we deemed ecologically relevant to our study species. Potential advantages of this approach are that it allows the identification of unexpected behavioral syndromes and focuses attention on ecologically important behaviors (Bell 2007). One important disadvantage, however, is the high rate of Type I errors (false positives) expected when conducting the many significance tests necessary to screen for correlations (Dochtermann and Jenkins 2007). The commonly used Bonferroni correction attempts to control the probability of arriving at one or more false positives (the family-wise error rate [FWER]) when conducting multiple significance tests. The Bonferroni correction controls Type I error but tends to incur high Type II error rates, meaning that some legitimate correlations (i.e., correlations that would reliably appear on repeated testing) are likely to be missed (Garcia 2004). A recently developed alternative to controlling the FWER is to control the false discovery rate (FDR; Benjamini and Hochberg 1995; Storey and Tibshirani 2003). The FDR is the proportion of significant features that are truly null. Controlling the FDR typically results in fewer Type I errors than uncontrolled multiple comparisons and fewer Type II errors than FWER controlled analyses. FDR algorithms allow researchers to quantify the proportion of significant comparisons that are truly null (q), in addition to the proportion of truly null comparisons judged to be significant (P). We controlled the FDR for our between-context comparisons because FDR control corresponds more closely with our research goals than FWER control or no control.

We produced a correlation matrix displaying the Pearson's correlation coefficients (r) for all 38 between-context correlations for the reduced variable set. The program Pop Tools version 2.7.5 (Hood 2006) was used to conduct randomization tests (10 000 replicates each) and generate P values for each test. We used the program Q Value (Dabney and Storey 2004) to determine the FDRs (q) associated with rejecting the null hypothesis in each of our hypothesis tests, in order of ascending P values (Storey 2002). We used this program with default settings (the tuning variable λ was allowed to range from 0 to 0.90 by intervals of 0.05). We interpreted comparisons with $P \leq 0.05$ and $q \leq 0.05$. After we identified a significant between-context correlation, we ran a PCA on the correlated variables to generate BT scores for each focal male.

Order effects

Behavioral syndrome studies are predicated on the assumption that the identity of the subject is the only relevant factor that is not independent among the observations that contribute to the correlation. Significant order effects indicate that an individual's experience in his first trial may have affected his performance in his second trial (e.g., "winner effects" and "loser effects"; Goessmann et al. 2000). If this were the case, trial experience might produce or exaggerate correlations in behavior between the 2 trials. Thus, behavioral correlations that do not account for possible order effects are not necessarily

indicative of behavioral syndromes. Indeed, the repeatability measures we report in this manuscript may be affected by intertrial dependency. We suggest that whenever possible, behavioral syndrome studies should vary trial order and test for order effects.

We used Monte Carlo tests to determine whether the order in which males experienced the assays affected the strength of the behavioral syndromes. For each significant correlation between behavior in 2 contexts, A and B, we separately determined the correlation coefficients (r) for males first subjected to assay A and males first subjected to assay B and subtracted the smaller value from the larger to determine $\Delta r_{\text{observed}}$. We then randomly shuffled males with respect to assay order and recorded the difference in correlation coefficients between A first and B first males ($\Delta r_{\text{randomized}}$). We repeated this process 10 000 times to create a distribution of Δr 's that would be expected given an absence of order effects (i.e., a null distribution). The proportion of this distribution that exceeded $\Delta r_{\text{observed}}$, multiplied by 2 (to account for the 2-tails of the distribution) represents the realized probability (P) of achieving $\Delta r \geq \Delta r_{\text{observed}}$ in the absence of order effects.

Morphological correlates

We tested whether variation in BT was related to morphological variation. The variables pronotum width, pronotum length, and average mass (averaged over weekly weighings) were subjected to PCA, and scores from the first principal component were considered a measure of overall size. We also ran a linear regression of average mass against an index of pronotum size (pronotum width \times pronotum length) to determine residual mass. We used randomized Pearson's correlations to compare PC1 (overall size) and residual mass to BT.

BTs and reproductive success

We attempted to relate individual males' BTs to their reproductive success resulting from the female assays. We compared the BTs of males that copulated versus those that failed to copulate using Mann-Whitney U -tests with randomization. We then compared the number of offspring with the BTs of the father among males that mated.

RESULTS

Data reduction

In the intruder assay, data from both the focal males and the opponent males produced 3 principal components with eigenvalues > 1 (Table 1). Butt, thrash, flip opponent, latency to thrash (negative), latency to butt (negative), chase, approach, and abdomen flick loaded heavily on the first principal component, which deemed "aggression toward male" because all these variables are offensive maneuvers. Climb walls and withdraw loaded strongly on the second principal component, which we deemed "retreat from male." The third principal component strongly emphasized thrust and hiss. These are both courtship behaviors, so we name this component "courtship toward male." We note that the behaviors thrust and hiss appear identical in male-male and male-female contexts.

We obtained 3 principal components with eigenvalues > 1 for the female assay (Table 2). Hiss, thrust, latency to thrust (negative) and latency to hiss (negative), loaded strongly on the first principal component, so we call this axis "courtship toward female." The second component is called "aggression toward female" and is characterized by high levels of thrash and approach. The third component gives a high loading to withdraw and lower loadings to hiss and thrust. We call this

Table 1
PCA of focal male (left half) and opponent male (right half) behavior during staged territory intrusions in the hissing cockroach *Gromphadorhina portentosa*

	Focal Males			Opponents		
	PC1 Aggression (43.6%)	PC2 Retreat (19.9%)	PC3 Courtship (13.7%)	PC1 Aggression (42.5%)	PC2 Retreat (15.0%)	PC3 Courtship (14.8%)
Flick	0.63	0.47	0.20	0.78	0.21	-0.03
Butt	0.93	0.12	-0.42	0.94	0.11	-0.09
Flip	0.84	-0.07	-0.07	0.75	0.14	-0.19
Chase	0.76	-0.27	-0.27	0.66	-0.03	-0.11
Thrash	0.91	-0.06	-0.11	0.83	-0.08	-0.14
Approach	0.67	-0.36	-0.02	0.67	0.06	0.01
Latency to butt	-0.80	-0.29	-0.02	-0.82	-0.06	-0.18
Latency to thrash	-0.84	0.01	0.00	-0.83	0.16	0.07
Withdraw	0.10	0.79	0.43	-0.04	0.85	0.38
Climb walls	0.01	0.80	0.38	-0.07	0.85	0.30
Hiss	0.13	-0.56	0.76	0.23	-0.39	0.82
Thrust	0.18	-0.52	0.78	0.22	-0.29	0.86

Component names (aggression, retreat, and courtship) are subjective titles based on patterns of factor loadings. Only principal components with eigenvalues ≥ 1 are considered. Numbers in parentheses below component names represent the percentage of variance in the factors explained by each principal component. Factor loadings with absolute values ≥ 0.5 are in bold font.

variable “retreat from female,” but we interpret this axis cautiously because it has a low eigenvalue (1.04), and a structure that resists simple classification.

In the foraging assay, latency to emerge and latency to eat contributed equally to the first principal component, which explained 96% of the variance in these 2 measures. We call this principal component “latency to forage.”

Within-context repeatability

Opponent males exhibited significantly repeatable levels of aggression ($N = 17, r = 0.64, P = 0.007$) but nonsignificantly repeatable levels of retreat ($N = 17, r = 0.31, P = 0.11$) and courtship ($N = 17, r = 0.34, P = 0.10$) during the intruder assays. They also elicited significantly repeatable levels of retreat ($N = 17, r = 0.70, P = 0.008$) and courtship ($N = 17, r = 0.43, P = 0.048$) but nonsignificantly repeatable levels of aggression ($N = 17, r = 0.37, P = 0.076$) from focal males. In other words, the levels of retreat and courtship that a focal male directed toward a given opponent in that opponent’s first trial predicted the levels of retreat and courtship that a different focal male would exhibit during the opponent’s second trial. Focal males’ latency to move and latency to right after moving were significantly repeatable in the righting trials (Table 3). Given the short intervals between righting trials,

however, we urge caution in the interpretation of these results and we do not discuss them further.

Behavioral syndromes

The FDR protocol for multiple comparisons recognizes 2 between-context behavioral syndromes. First, a “fast–slow” syndrome is evidenced by a positive correlation between latency to move in a righting context and latency to forage in a foraging context ($N = 67, r = 0.38, P < 0.001, q = 0.018$). Thus, males that rapidly emerge from a shelter to feed also begin moving quickly after being placed on their dorsum. Second, there was a positive association between courtship toward male and courtship toward female ($N = 69, r = 0.34, P = 0.003, q = 0.032$), which we call a “libido” syndrome. The q value 0.032 indicates “the expected proportion of false positives among the tests found to be significant” (Dabney and Storey 2004, p. 8). Thus, we claim high confidence that both “fast–slow” and libido represent repeatable correlations, rather than statistical artifacts. Data from the saline assay were not significantly correlated to data from any of the other assays.

Order effects

We tested whether the 2 between-context behavioral correlations that we identified might have been spurious results based on order effects (see Order effects in Methods). We did not find statistically significant effects of assay order on the

Table 2
PCA of male courtship behavior in the hissing cockroach *Gromphadorhina portentosa*

	PC1 Courtship (45.4%)	PC2 Aggression (25.8%)	PC3 Retreat (14.9%)
Thrust	0.87	-0.11	0.30
Hiss	0.88	-0.09	0.05
Latency to hiss	-0.74	0.11	0.51
Latency to thrust	-0.83	0.10	0.41
Thrash	0.27	0.92	0.09
Approach	0.26	0.92	0.07
Withdraw	0.52	-0.28	0.72

See Table 1 legend for details.

Table 3
Intra-individual repeatability (Pearson’s r) for latency to move and latency to right after moving in self-righting trials of male hissing cockroaches

	1 versus 2 ($N = 64$)	2 versus 3 ($N = 65$)	1 versus 3 ($N = 67$)
Latency to move	0.33 (0.0056)	0.63 (<0.0001)	0.57 (<0.0001)
Latency to right after moving	0.41 (<0.0001)	0.62 (0.0006)	0.45 (<0.0001)

Each of the P values shown in parentheses were derived from 10 000 Monte Carlo simulations.

relationships between latency to forage and latency to move (Monte Carlo test with 10,000 randomizations; $\Delta r_{\text{observed}} = 0.01$, $P = 0.99$) or courtship toward male and courtship toward female (Monte Carlo test with 10 000 randomizations; $\Delta r_{\text{observed}} = 0.46$, $P = 0.11$).

Morphological correlates

In our PCA of morphological variables, pronotum width, pronotum length, and average weight all loaded heavily onto the first principal component (all factor loadings >0.78), which explained 76% of the overall variance in the data. We therefore termed PC1 from this analysis size. Fast–slow scores were not significantly related to size (Pearson's correlation with randomization: $N = 67$, $r = -0.12$, $P = 0.34$) or residual mass ($N = 67$, $r = -0.09$, $P = 0.47$). Libido was not significantly correlated with size ($N = 69$, $r = -0.08$, $P = 0.47$) or residual mass ($N = 69$, $r = 0.22$, $P = 0.07$).

BTs and reproductive success

Focal males' fast–slow scores did not predict their copulation success during the female assay (Mann–Whitney test with randomization: $N = 67$, $U = 496$, $P = 0.46$). Libido scores were not compared with copulation success because measures that contributed to libido came from the female assay. Because copulation is exclusive to all other measured behaviors in the female assays, the rates of these behaviors are not independent of the occurrence of copulation. Among males that mated, fast–slow scores were not correlated to the number of offspring resulting from the female assays ($N = 37$, $r = 0.082$, $P = 0.62$). Libido, however, correlated positively with the number of offspring ($N = 39$, $r = 0.40$, $P = 0.0084$; Figure 1).

DISCUSSION

A behavioral syndrome that we term “libido” links males' behavior in the context of female choice (i.e., the choice to copulate or not to copulate) to their behavior in the context of male–male competition. Specifically, males that courted females intensely also tended to court other males. This finding supports the hypothesis that behavioral syndromes encompass sexually selected behaviors. To our knowledge, the libido

syndrome described in this report represents the first known behavioral syndrome positively linking sexual response toward males and females. A male's libido score predicted the number of offspring that resulted from a single mating event. It is worth noting, however, that the relationship between libido and number of offspring could be context dependent, and we do not know how courtship intensity affects fitness under natural conditions. It may be the case that females exert cryptic choice (Sheldon 2000) based on a male's courtship performance or some unmeasured trait related to his courtship performance. Alternatively, courtship intensity may covary with some component of male fertility (e.g., sperm motility), or females may exert some control over courtship intensity which is linked to their reproductive investment. The nearly significant positive relationship between residual mass and libido ($P = 0.07$) suggests that body condition may play some role in determining libido.

Male–male courtship in cockroaches has been attributed to chemical and/or behavioral female mimicry by the courted male (Wendelken and Barth 1985). A common adaptive explanation for female mimicry is that it prevents aggression from dominant males and distracts competitors from courting receptive females (reviewed in Forsyth and Alcock 1990; Shine et al. 2000). Given the intense intrasexual competition in this species (Guerra and Mason 2005) and the pronounced large male advantage in winning contests (Clark and Moore 1995), it seems reasonable that inferior competitors might benefit from mimicking females if they could avoid aggression and so maintain access to fertile females. Even if this system is not an example of adaptive female mimicry, males that court other males may be maladaptively responding as if the target were actually a female (Harari et al. 2000; Eliyahu et al. 2007).

If male–male courtship is indeed maladaptive, the libido syndrome may represent an example of “behavioral spillover.” Behavioral spillover occurs when selection favors a suite of covarying behaviors with adaptive results in one context but maladaptive results in another (Riechert and Hedrick 1990; Sih, Bell, and Johnson 2004; Sih, Bell, Johnson, and Ziemba 2004; Johnson and Sih 2005; Quinn and Cresswell 2005; Duckworth 2006). Recall that high libido males courted both females and males more intensely than low libido males. Males with high libido scores also fathered more offspring in a controlled mating experiment, suggesting that libido is under positive selection in the male–female context. Male-directed courtship may be maladaptive, given the energy expended, the opportunity costs, and the costs of allowing potential rivals to remain in the vicinity. We hypothesize that evolution has not decoupled courtship intensity in a male–female context from courtship intensity in a male–male context and that certain males take advantage of this pattern by imitating females (e.g., chemically, behaviorally) to avoid aggression. Implicit in this hypothesis is the idea that a behavioral syndrome has driven the evolution of alternative reproductive strategies. A logical next step in this line of research would be to quantify the costs and benefits associated with different levels of libido in a quasi-natural colony setting.

We chose to name the syndrome linking latency to move and latency to forage fast–slow rather than, for example, proactive–reactive (Koolhaas et al. 1999), shy–bold (Wilson et al. 1994), or exploration–avoidance (Dingemanse et al. 2007) because fast–slow is minimally connotative (for a similar syndrome in chicks, see Groothuis and Carere 2005, p. 145). We do not intend to imply that this syndrome is related to other identified syndromes sharing the name fast–slow (e.g., Verbeek et al. 1994), beyond the fact that fast individuals tend to behave faster than slow individuals in more than one context. We did not find a significant relationship between aggression and the variables that contributed to fast–slow. In contrast,

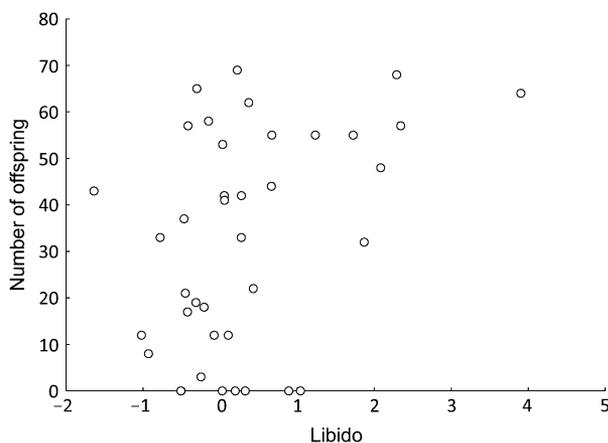


Figure 1 Libido score correlated positively with the number of offspring fathered among male hissing cockroaches that mated in staged 30 min encounters with females (Pearson's correlation with randomization: $N = 39$, $r = 0.40$, $P = 0.0084$). Libido is a behavioral syndrome (see text).

similar syndromes called fast–slow or shy–bold have been linked to aggression in great tits, *Parus major* (e.g., Verbeek et al. 1996; Drent 2003), sticklebacks, *Gasterosteus aculeatus* (Huntingford 1976, 1982; Bell 2005), fishing spiders, *Dolomedes triton* (Johnson and Sih 2005), and field crickets, *Gryllus integer* (Kortet and Hedrick 2007). We therefore conclude that the fast–slow syndrome in hissing cockroaches is not homologous to the syndromes described in those species.

We found no relationship between the number of hisses elicited during the saline assay and the behavioral measures in the other 4 contexts. Taken at face value, this lack of a relationship indicates that reactivity is independent of the other measured behaviors. Alternatively, our assay may have failed to capture a biologically relevant aspect of reactivity, or it may have failed to measure individuals' reactivity with sufficient precision given that we only measured each male's reactivity one time.

Even with relatively modest sample sizes ($N = 17$), we found strong evidence that aggression directed toward an opponent and retreat and courtship elicited from an opponent were repeatable within males. The design of our study does not allow us to determine whether these results are due to stable individual differences (i.e., "personalities" or BTs) or the influence on the first trial on the second. Further complicating the interpretation of these results, variability in opponents may influence the behavior of focals, and vice versa. Regardless of its cause, however, the existence of within-individual repeatability of behavior and repeatable reactions from conspecifics raises interesting questions about the role of stable BTs in social dynamics. We are conducting experiments to determine whether the repeatability of aggressive behavior and the ability to elicit retreat and courtship behaviors in conspecifics persists in a colonial environment. If this is the case, it may be possible to link BTs to dominance hierarchies, mating skew, and other group-level phenomena (Weinstein and Maelzer 1997; Sih and Watters 2005; Nemiroff and Despland 2007; Nonacs and Kapheim 2007).

In male hissing cockroaches, sexual behavior toward other males, sexual behavior toward females, and the reproductive benefits of mating are nonindependent. Our findings contribute to a growing body of evidence that suggests that correlations between behavioral traits, especially those traits involved in sexual behavior, affect the evolution of behavior.

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