

Developmental Environment Affects Risk-Acceptance in the Hissing Cockroach, *Gromphadorhina portentosa*

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Consistent individual differences in the tendency to accept risk have been demonstrated in invertebrates, fish, birds, and mammals, including humans. These individual differences have been associated with size, growth rate, survival, and reproductive success. Little research, however, has investigated the effect of developmental environment on individual differences in risk-acceptance. Competing hypotheses offer different explanations of how variation in the quality of the developmental environment affects risk-acceptance in adults. The first hypothesis states that individuals developing in poor quality environments take risks because such behavior is their only means of obtaining adequate fitness returns. The second hypothesis states that individuals developing in poor environments avoid risk because their poor physical condition makes them especially vulnerable to injury or death. We measured several forms of risk-accepting behavior (exploration, foraging, and recovery after disturbance) in male hissing cockroaches (*Gromphadorhina portentosa*) that had developed in nutritional and social environments of varying quality. Individuals raised on poor nutrition diets exhibited lower levels of risk-acceptance than those raised on high nutrition diets. Risk-acceptance among individuals that developed on poor nutrition diets was negatively correlated with body size. We conclude that quality of developmental environment affects risk-acceptance across behavioral contexts in male hissing cockroaches. Our findings are consistent with the hypothesis that condition-dependent vulnerability mediates the relationship between developmental environment and risk-acceptance.

Keywords: behavioral syndromes, risk, shy-bold axis, boldness, personality in animals

Consistent individual differences in behavior have been demonstrated in diverse taxa, including arthropods, cephalopods, and vertebrates (reviewed in Gosling & John, 1999; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004). Individual differences can be measured with respect to a single behavior, but they are particularly interesting when they involve more than one behavior and/or more than one behavioral context (e.g., exploration and aggression). Correlations between behaviors across contexts are called *behavioral syndromes* (Sih, Bell, & Johnson, 2004). Although traditional behavioral ecological models of optimality suggest that natural selection favors different behavioral optima in different contexts, consistent individual differences in

behavior may constrain the degree to which individuals can exhibit optimal behavior in all situations (Bell, 2007). Therefore, understanding the causes and consequences of stable individual differences in nonhuman animals represents an important step forward in the behavioral sciences.

An important axis of behavioral variation that has been demonstrated in many animal taxa is risk-acceptance. Risk-acceptance is defined as behavior associated with boldness, including exploration, food acquisition, and recovery from disturbance (Brown & Braithwaite, 2004; Coleman & Wilson, 1998; Sinn, Gosling, & Moltschanivskyj, 2008; Wilson & Godin, 2009; Wolf, van Doorn, Leimar, & Weissing, 2007). Individual differences in risk-acceptance have been demonstrated in invertebrates (Sinn, Perrin, Mather, & Anderson, 2001), fish (Bell & Stamps, 2004), birds (van Oers, Drent, de Goede, & van Noordwijk, 2003), and mammals (Reale & Festa-Bianchet, 2003), including humans (Zuckerman, 2007).

Although several variables have been shown to correlate with risk-acceptance, including size (Brown & Braithwaite, 2004), growth rate (Ward, Thomas, Hart, & Krause, 2004), survival (Dingemanse, Both, Drent & Tinbergen, 2004), and reproductive success (Both, Dingemanse, Drent, & Tinbergen, 2005; reviewed in Sinn et al., 2008; van Oers et al., 2003), little empirical work has been conducted on the role of developmental environment in facilitating the emergence of risk-related behavioral syndromes. Some previous studies have investigated consistency of risk-accepting behavior across the life span (Bell & Stamps, 2004; Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005; Sinn et al., 2001, 2008), but we know of only one study in which researchers

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manipulated juvenile developmental environment to investigate its effect on risk-acceptance in adulthood. That study demonstrated that in the great tit, poor nutrition during development can facilitate increased exploration among individuals in a genetic line selected for “slow” behavior (Carere, Drent, Koolhaas, & Groothuis, 2005).

Intraspecific variation in risk-acceptance may develop as a result of life-history tradeoffs contingent on developmental environment (Mishra & Lalumière, 2008; Roff, 2002; Stamps, 2007; Wolf et al., 2007). Variation in the relative value of current versus future reproduction may lead to the evolution of populations in which individuals vary with respect to risk-acceptance in more than one behavioral context, generating a correlation in behavior across contexts (Stamps, 2007). Individuals with high quality future prospects may be less risk-accepting than individuals with low quality future prospects because individuals with high quality future prospects have more to lose by engaging in risk-accepting behaviors. Consequently, as animals gain information about their own probable current and future reproductive value, they should adjust their levels of risk-acceptance.

Future reproductive prospects may be assessed through both exogenous environmental cues (e.g., conspecific sex ratio, nutritional availability), and endogenous cues of competitive ability (e.g., size, body condition). A male-skewed population, for example, may serve to indicate high levels of intraspecific male-male competition for resources and mates. An environment with poor food availability may similarly signal limited resources, facilitating increased competition and greater risk-acceptance. Poor food availability may also lead to the development of adults that are smaller or are in poorer condition compared to those that developed under high nutrition conditions. Individuals that are in poorer condition may engage in increased risk-accepting behavior to more ably compete with conspecifics. If intraspecific variation in future prospects drives the expression of risk-acceptance, individuals that develop in high quality environments should be risk-averse relative to those that develop in low quality environments.

Alternatively, individuals that are larger or in superior condition may be able to engage in behaviors that would entail unacceptable costs to individuals that are smaller or in poorer condition, including such risk-accepting behaviors as exploration or food acquisition (e.g., Brown, Jones, & Braithwaite, 2007; Lopez, Hawlena, Polo, Amo, & Martin, 2005; Mishra & Lalumière, 2008). High quality individuals may thus expose themselves to a lower probability of harm or death while engaging in risky behavior that may yield fitness benefits (e.g., outcompeting conspecifics for food by foraging more per unit time; Sih & Bell, 2008). Some previous research suggests that individuals in better condition are better able to successfully engage in risky behavior (e.g., Bliege-Bird, Smith, & Bird, 2001; Candolin & Voigt, 2001; Reaney & Blackwell, 2007; Smith, Bliege-Bird, & Bird, 2003). Thus, if risk-acceptance is condition-dependent, then individuals from high quality environments should be risk-accepting relative to those that develop in low quality environments.

We investigated whether quality of developmental environment influences the development of risk-accepting behavior in a laboratory colony of Madagascar giant hissing cockroaches (*Gromphadorhina portentosa*, “hissing cockroaches” hereafter). Hissing cockroaches are sexually dimorphic, colonial insects that exhibit substantial variation in adult morphology and behavior, and are

easily reared, making them an excellent laboratory study species. We subjected developing male hissing cockroaches to one of two nutritional regimes (high or low nutrition) and one of two social regimes (female or male companions) according to a factorial design. We then measured their behavior in assays that measured risk-acceptance, aggression, and sexual behavior. We used these data to test the competing predictions of the hypotheses that variation in risk-acceptance is driven by (1) cues of future reproductive prospects in the developmental environment, or (2) the physical ability to engage in risk-accepting behaviors without incurring high costs.

Method

Study Animals

Study animals were obtained from a breeding colony founded by animals purchased from VWM Reptiles (Edinburg, IL). When animals began to exhibit sexual dimorphism in the subgenital plate, they were removed from the breeding colony and placed in same-sex juvenile colonies. Focal males that appeared to have undergone the penultimate molt were weighed, measured, and isolated in plastic boxes (21 × 14 × 10 cm). Maximum pronotum width and length were measured with digital calipers (Mitutoyo SC-6”). Immediately after isolation, focal males were randomly assigned to one of four treatment conditions (see below), marked with correction fluid, and monitored to determine whether they had molted again. Males incorrectly identified as being in the penultimate instar were excluded from the study. Eighty-six focal males completed the treatments and behavioral assays.

Large, recently molted females were deemed “putative adults” and housed with other putative adult females that molted on the same day. These females were marked with correction fluid and monitored for additional molts. All females were provided with a cardboard egg crate shelter, an *ad libitum* supply of water and food (Purina Dog Chow; Nestle Purina Pet-Care company, St. Louis, MO), and a weekly supplement of carrots. Animals were maintained in a 12:12h reversed light/dark cycle at 28 °C and 50% humidity throughout the experiment.

Treatment Conditions

Focal males in the penultimate instar were randomly assigned to one of four treatment conditions according to a two by two factorial design. The factor “nutrition” was either high ($n = 42$) or low ($n = 44$), and the factor “companion” was either male ($n = 44$) or female ($n = 42$). Males in the high nutrition group received feed made by grinding Purina Dog Chow (Nestlé Purina Pet Care Company, St Louis, MO) with water. This mixture was formed into cakes approximately one centimeter thick and allowed to air dry. Males in the low nutrition group received feed that was identical, except that 50% of the dog chow (by weight) was replaced with indigestible alpha-cellulose (Sigma Aldrich, Inc., St. Louis, MO). Males in both conditions received water and feed *ad libitum*. Males in the high nutrition condition also received one gram of peeled carrot every week. Social companions consisted of either two adult males or two adult females, chosen at random from the breeding colony. Males remained in treatment until their

adult molt. After the adult molt, all focal males received *ad libitum* supplies of feed made from unadulterated dog chow.

Behavioral Assays

Beginning two weeks after their final molt, each of the 86 focal males was subjected to six randomly ordered behavioral assays at one week intervals. Three of the assays (disturbance, foraging, and exploration) measured risk-acceptance in potentially stressful situations. Intruder and female assays allowed us to examine correlates of risk-acceptance in the context of sexual selection. The five assays are described in more detail below.

All assays were conducted in a heated (28 °C) room separate from the animal housing area, and were recorded by an overhead video camera (Sony Handicam DVD103, Sony Electronics Inc., San Diego, CA). Trials conducted in the dark utilized near-infrared illumination for recording. Container walls were coated with a mixture of petroleum jelly and mineral oil to prevent escape. For trials that involved the male staying in his enclosure, all objects in the enclosure were removed. The foraging, intruder, and female assays were adapted from Logue, Mishra, McCaffrey, Ball, and Cade (2009). Data from each assay were scored by a single observer blind to treatment condition and to the performance of the focal male in other assays. Exploration, intruder, and female trials were scored using JWatcher 1.0 (Blumstein, Daniel, & Evans, 2006).

Disturbance. The “disturbance” assay measured risk-acceptance in a postdisturbance context. Focal males were placed in an opaque plastic tube (diameter = 4.25 cm; length = 11 cm) and a snap-on lid was used to cover the tube. The tube was then rolled back and forth three times (amplitude = 18 in; frequency = 0.5 Hz), and placed in the focal male’s enclosure in the dark trial room. The lid of the tube was then removed. An observer recorded time that elapsed between the removal of the lid and the emergence of the animal’s head from the tube, and from that time until the tip of the animal’s abdomen left the tube.

Foraging. The “foraging” assay measured risk-acceptance in a foraging context. Prior to testing, the focal male was deprived of food for 48 hours. At the beginning of the assay, the male was placed under an opaque cup (diameter = 10 cm; length = 3.5 cm) at one end of their enclosure. A removable door (height = 2 cm; width = 3.6 cm) on one side of the cup was attached to the cup using hook and loop fabric. One gram of previously frozen banana (a highly desirable food to this species; Logue et al., 2009) was placed on a food dish five centimeters away from the removable door. After a five-minute acclimation period, the door was removed. The time it took for the male to emerge from the shelter and begin consuming the food item was termed “latency to eat.” A value of 1800 seconds (the maximum length of the trial) was recorded if the male failed to emerge.

Exploration. The “exploration” assay measured risk-acceptance in the context of exploring a novel environment. The bottom of a plastic container (72 × 78 × 38 cm) was marked with a grid (2 × 2 cm squares). Focal males were placed in the center of the container under an opaque round shelter (diameter = 11 cm; length = 7.5 cm) and left to acclimate for five minutes in a dark room. The opaque container was then removed, and the focal male was left to explore the container for 15 minutes. Trial videos were scored for the number of new squares explored (counted when a

male entered a square that he had not visited previously), old squares explored (scored when a male entered a square that he had visited previously), number of times the male climbed the wall, and the total time spent climbing.

Intruder. The “intruder” assay measured behavior in response to the presence of a male intruder in the focal male’s enclosure. Focal males were size-matched with opponent males based on the size index $\text{pronotum width} \times \text{pronotum length}$. Opponent males were never used as focal males. Some opponent males were used for multiple trials to facilitate size matching (as in Bell & Stamps, 2004; Logue et al., 2009). Opponent males were given at least two days to recover between intruder trials. Focal males were given five minutes to acclimate to the dark trial room. The experimenter then introduced the opponent into the focal male’s enclosure, and forced the two males to touch antennae. Males were allowed to interact for 15 minutes. Observers scored trial videos for several behaviors in the focal male: abdomen flick (abdomen moves laterally to strike), butt (posterior— anterior strike with the pronotum), flip opponent (abdomen flick or butt causes the opponent to land on its dorsum), chase, thrash (lateral thrashing of the abdomen against the substrate; each cycle was counted as one thrash), approach, withdraw, climb walls, hiss, and thrust (anterior—posterior movement of the abdomen). All measures were taken from Logue et al. (2009).

Female. The “female” assay measured behavior in the presence of a virgin female. After a five minute acclimation period in a dark room, a virgin female (age 14 to 29 days after an adult molt) was introduced into the focal male’s enclosure and the two animals were made to touch antennae. Each female was used in only one trial. Trials were 30 minutes long. Observers scored trial videos for focal male behavior, including thrusts, hisses, thrashes, approaches, and withdrawals. Trials ended if the pair copulated, and all variables were divided by time to copulation (or 1800 s if the pair did not copulate) to produce rates of behavior.

Morphology

Composite measures of size at the onset of experimental treatment (hereafter, *preadult size*) and size at adulthood (hereafter, *adult size*) were computed by conducting principal components analyses (PCAs) without rotation on pronotum length, pronotum width, and body mass. Two growth rates were calculated, one for the period during treatment, and one for the period of trials (early adulthood). Growth rate during treatment was calculated using the formula $(\text{mass at adult molt} - \text{mass at treatment isolation})/\text{days from preadult molt to adult molt}$. Growth rate during trials was calculated using the formula $(\text{mass at final trial} - \text{mass at adult molt})/\text{days from adulthood to last trial}$.

Results

Data Preparation and Reduction

Several variables were positively skewed and were corrected with logarithmic transformations. Nontransformed means are reported, with the exception of PCA results which reflect analyses involving transformed values. Days to adulthood could not be normalized so nonparametric tests were used for analyses involv-

ing this variable. Nonparametric techniques were employed for all analyses involving copulation.

We conducted separate PCAs for exploration, intruder, and female trials following protocol derived from other studies of behavioral syndromes (e.g., Logue et al., 2009; Sinn, Gosling, & Moltchanowskyj, 2008; Wilson & Godin, 2009). This methodology reduces the number of variables used in subsequent analyses, increases degrees of freedom within PCA analyses, and facilitates the use of single reliable scores for target behaviors (Sinn et al., 2008).

The two disturbance measures were not correlated, so a composite variable was computed by summing the two measures within the disturbance assay. All PCAs were conducted without rotation. Principal components with eigenvalues >1 are reported; all principal component structures were verified through the use of scree plots. We reversed latency to eat and latency to recover following disturbance by multiplying by -1 for all analyses, so that for all risk-acceptance measures, a higher score indicated more risk-acceptance. All statistical tests are two-tailed unless otherwise specified. Values in brackets for statistical tests represent degrees of freedom.

We found one PC with eigenvalue >1 for preadult size and one for adult size. The preadult size PC explained 55.4% of variance, with all loadings $> .545$ and positive. The adult size PC explained 75.2% of variance, with all loadings $> .847$ and positive.

A single PC with eigenvalue >1 explained 75.7% of the variance in exploration behaviors (amount of time climbing, number of climbs, number of old squares traversed, number of new squares traversed; all loadings $> .840$ and positive). This PC was termed “exploration.”

Three PCs with eigenvalues >1 explained 76.1% of variation in focal male behavior in the intruder assay (see Table 1). Aggressive behaviors (flick, butt, flip, chase, thrash, and approach) loaded heavily on the first component, termed “aggression.” Hiss and thrust behaviors loaded heavily on the second component. Because hiss and thrust behaviors are both courtship behaviors, we termed this component “male-male courtship” (after Logue et al., 2009). Climbing and withdrawal behaviors loaded heavily on the third component, termed “withdrawal.” A scree plot suggested that the

“withdrawal” component was not particularly robust. As a consequence, we do not discuss it further.

A PCA on behaviors in the female assays indicated two PCs with eigenvalues >1 , explaining 68.7% of variance (see Table 2). Hiss and thrust loaded heavily on the first component, termed “courtship toward female.” Approach and withdrawal behaviors loaded heavily on the second component, termed “activity around female.”

Development and Morphology

Preadult size was positively correlated with adult size, $r(84) = .396, p < .001$. Cockroaches in the high nutrition condition took less time to develop and were larger at adulthood, but neither difference was significant; days to adulthood: *Mann-Whitney U test*, $z = -.372, p = .71$; size at adulthood: $t(84) = 1.35, p = .18$. None of pronotum width, pronotum length, or mass significantly differed as a function of nutrition condition (all $t_s < 1.72, p_s > .09$). Growth rate during treatment and during the trials did not significantly differ based on nutrition condition (both $t_s < 1.27, p_s > .21$). Social condition had no effect on days to adulthood, *Mann-Whitney U test*, $z = -.298, p = .77$. Size at adulthood and growth rate also did not significantly differ based on nutrition condition (both $t_s < .53, p_s > .60$). Descriptive statistics for developmental and morphological variables are presented in Table 3.

Development and Risk-Acceptance

We conducted correlations between the three variables involving risk-acceptance: latency to eat, latency to recover following disturbance, and exploration. Latency to eat was significantly correlated with both latency to recover following disturbance, $r(84) = .240, p = .01$, and with exploration, $r(84) = .210, p = .03$. Exploration was correlated with latency to recover after disturbance, but not significantly $r(84) = .135, p = .11$ (all tests one-tailed). We conducted a PCA to see if a single component explained variance among risk-acceptance variables. A single PC, which we called “risk-acceptance,” explained 46.4% of the variance in these measures (see Table 4). Descriptive statistics for each of the individual variables involving risk-acceptance and the risk-acceptance component are presented in Table 3.

Correlations between the three variables involving risk-acceptance may have been influenced by order effects (Logue et al., 2009). If an individual’s experience in an earlier trial affected subsequent behavior, correlations between the three risk-acceptance behaviors (and thus, the risk-acceptance behavioral syndrome) may have been exaggerated. To test for order effects, we compared the magnitude of the correlation obtained for assays presented in different orders. For example, for two assays, A and B, we compared the magnitude of the correlation between A and B when A came first with the magnitude of the correlation between A and B when B came first, using Fisher’s z test. Statistically significant order effects were not observed for the correlations between latency to eat and latency to recover following disturbance, $Z = -.17, p = .97$, latency to eat and exploration, $Z = -.93, p = .35$, or exploration and latency to recover following disturbance, $Z = 1.22, p = .22$.

To investigate whether risk-acceptance was affected by developmental environment, a nutrition condition (high, low) by social

Table 1
Component Loadings for PCA of Focal Male Behavior in the Intruder Assay

	Aggression (46.6%)	Courtship (17.1%)	Withdrawal (12.4%)
Flick	.803	-.088	.162
Butt	.951	.036	-.073
Flip	.882	.019	-.231
Chase	.926	-.045	-.093
Thrash	.758	.007	-.005
Approach	.894	.167	-.102
Hiss	.011	.878	.210
Thrust	.019	.869	.264
Withdraw	.270	-.294	.726
Climb walls	.172	-.237	.704

Note. Only principal components with eigenvalues ≥ 1 are shown. Numbers in parentheses represent the percentage variance explained by the principal components. Loadings $> .50$ are in bold.

Table 2
Component Loadings for PCA of Focal Male Behavior in the Female Assay

	Courtship (35.8%)	Activity (32.9%)
Butt	-.245	.076
Approach	-.168	.881
Withdraw	-.138	.894
Hiss	.928	.082
Thrust	.908	.235

Note. Only principal components with eigenvalues ≥ 1 are shown. Numbers in parentheses represent the percentage variance explained by the principal components. Loadings $> .50$ are in bold.

condition (male, female) two-level full factorial analysis of covariance (ANCOVA) was conducted on risk-acceptance, with morphological and growth rate variables as covariates (adult size, preadult size, growth rate during treatment, growth rate during adulthood). There was no significant main effect of social condition on risk-acceptance, $F(1, 78) = 1.51, p = .21, \eta^2 = .02$ (Figure 1, Table 3). A main effect of nutrition was observed, however, indicating that cockroaches that developed under low nutrition conditions exhibited significantly lower levels of risk-acceptance than those that developed under high nutrition conditions, $F(1, 78) = 5.29, p = .02, \eta^2 = .06$ (Figure 1, Table 3). The social condition by nutrition interaction and all covariates were not significant (all $F_s < 2.81, p_s > .10$).

Our data seemed to contradict some previous findings indicating that body size is often associated with risk-acceptance (e.g., Brown & Braithwaite, 2004; Brown et al., 2007; Lopez et al., 2005), so we explored this relationship further. We found that adult size was negatively and significantly associated with risk-acceptance within the low nutrition condition, $r(42) = -.394, p = .008$, but not the high nutrition condition, $r(40) = -.003, p = .98$, a marginally significant difference in correlation magnitude, Fisher's $z = 1.71, p = .06$ (see Figure 2). No significant association between risk-

Table 3
Means [and 95% Confidence Intervals] for Developmental and Morphological Variables, and Risk-Acceptance Assays

	High nutrition		Low nutrition	
	Male company ($N = 20$)	Female company ($N = 24$)	Male company ($N = 22$)	Female company ($N = 20$)
Development and morphology				
Days to adulthood	91 [42, 139]	88 [48, 127]	71 [49, 93]	64 [51, 78]
Mass (Adulthood)	8.6 [7.7, 9.4]	7.9 [7.2, 8.6]	7.6 [6.9, 8.2]	8.1 [7.0, 9.1]
Pronotum size (adulthood)	373.3 [350.2, 396.4]	362.5 [340.0, 385.1]	340.4 [319.2, 361.6]	367.7 [338.7, 396.7]
Size (adulthood) (PC)	.29 [-.17, .75]	.02 [-.38, .42]	-.35 [-.71, .02]	.10 [-.45, .66]
Growth rate (treatment)	.06 [.04, .09]	.05 [.04, .07]	.05 [.04, .07]	.06 [.04, .08]
Growth rate (trials)	.04 [.03, .05]	.03 [.02, .05]	.04 [.03, .05]	.05 [.03, .06]
Risk-acceptance assays				
Exploration (PC)	-.02 [-.47, .42]	.32 [-.17, .81]	-.23 [-.67, .19]	-.05 [-.45, .36]
Latency to eat	320 [151, 490]	193 [77, 311]	307 [179, 434]	384 [215, 554]
Disturbance recovery	1060 [480, 1641]	782 [303, 1262]	1547 [874, 2220]	1405 [655, 2155]
Risk-acceptance (PC)	.003 [-.50, .51]	.46 [.05, .88]	-.23 [-.62, .16]	-.23 [-.69, .22]

Note. All means presented are non-transformed. Pronotum size was obtained by multiplying pronotum length with pronotum width. Mass is in grams. Latency to eat and disturbance recovery are in seconds (lower scores = more risk-acceptance). Size at adulthood, exploration, and risk-acceptance are represented by principal component scores.

Table 4
PCA of Risk-Related Behaviors

	Risk-acceptance (46.7%)
Exploration	.627
Food	.743
Disturbance	.669

Note. Only principal components with eigenvalues ≥ 1 are shown. Numbers in parentheses represent the percentage variance explained by the principal components. Loadings $> .50$ are in bold.

acceptance and body size was observed in either social condition (both $r_s < .27, p_s > .09$).

Risk, Aggression, and Reproductive Behavior

Previous studies have demonstrated significant relationships between risk-acceptance and aggression. In this study, aggression in the intruder trial was not significantly correlated with any of the individual behaviors comprising risk-acceptance (latency to eat, exploration, and recovery from disturbance), nor with the risk-acceptance component (all $r_s < .16, p_s > .15$).

Of the 14 males that copulated, 11 sired offspring. Risk-acceptance did not significantly differ between males that successfully copulated and those that did not, Mann-Whitney U test, $z = -1.05, p = .29, M_{\text{copulate}} = .29, M_{\text{noncopulate}} = -.05$.

Discussion

A between-context behavioral syndrome that we call risk-acceptance explained interindividual variance in risky behaviors across three ecologically relevant contexts (exploration, foraging, and latency to recover from disturbance) in male hissing cockroaches. Developmental environment had a significant effect on the expression of risk-acceptance: Cockroaches that developed on high quality diets exhibited significantly higher levels of risk-acceptance in adulthood than those that developed on low quality

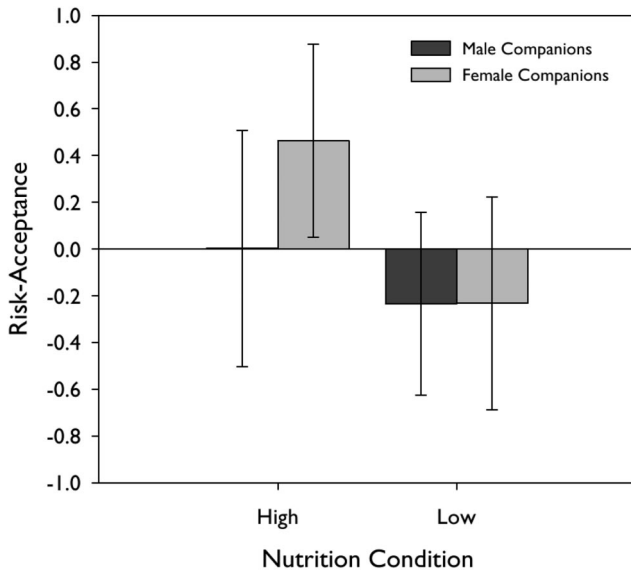


Figure 1. Mean risk-acceptance as a function of nutrition condition during development. Confidence intervals (95%) are indicated by the error bars.

diets. These results are consistent with the hypothesis that variation in individuals' ability to safely engage in risky behavior drives covariation in risk-acceptance across contexts (i.e., a risk-acceptance behavioral syndrome).

Defining Risk-Acceptance

Several different terms have been used to name behavioral syndromes involving risk-accepting behavior, including risk-taking (e.g., van Oers et al., 2003), shy-bold (or boldness; Wilson, Clark, Coleman, & Dearstyne, 1994), proactive-reactive (Koolhaas et al., 1999), exploration-avoidance (Dingemanse et al., 2007), activity (Brodin, 2009), and fast-slow (Groothuis & Carere, 2005; Logue et al., 2009), among others. Although differently named, each of these syndromes reflects risk-acceptance, where risk-acceptance simply refers to behaviors that expose individuals to relatively high outcome variance. For example, an individual that engages in increased exploratory behavior is likelier to experience higher variability in potential outcomes (e.g., suffering from predation, finding a superior food patch) than an individual that does not engage in such exploratory behavior. Therefore, we chose to name the syndrome linking exploration, disturbance recovery, and latency to eat in this study risk-acceptance because it is a general term that encompasses other characterizations of bold, fast, proactive, or exploratory behavior.

Nutrition

Males that received high quality food during development exhibited higher levels of risk-acceptance than males that received low quality food. Males raised on high nutrition may have engaged in more risk-accepting behavior because they possessed better physical condition, mitigating the costs of risky behavior. Condition reflects several different components of body composition,

including fat, lean dry mass, and water, but is usually estimated from body mass and size (Schulte-Hostedde, Zinner, Millar, & Hickling, 2005). In this study, animals that developed in a high nutrition environment (compared to a low nutrition environment) were larger at adulthood, but this effect was not significant. It is possible, however, that unmeasured aspects of condition may have been associated with patterns of risk-accepting behavior.

Size did not predict risk-acceptance across nutrition conditions. Among individuals that experienced low nutrition, however, smaller size was significantly associated with increased risk-acceptance. It is possible that larger males in the low nutrition group invested limited resources into growth, necessitating less investment in body condition (e.g., investment in neural and/or muscular development, nutritional/energetic stores). Such individuals may have been more vulnerable and thus less risk-accepting than smaller low nutrition males that invested less into growth and more into body condition. Further research is necessary to investigate this hypothesis. Incorporation of measures of body condition independent of size in future studies may more effectively shed light on the relationship between body condition and risk-acceptance.

Social Environment

If quality future reproductive prospects are associated with reduced risk-acceptance, the presence of female company during development—a cue of positive future reproductive prospects—should reduce risk-acceptance. We did not find support for this hypothesis, in that social condition had no significant effect on the development of risk-accepting behavior. If, however, risk-acceptance is largely condition dependent, then our results suggest that variation in social company during development would influence risk-acceptance only if such company affected condition. We found that social company had no effect on condition, and therefore it is unsurprising that social condition did not affect risk-

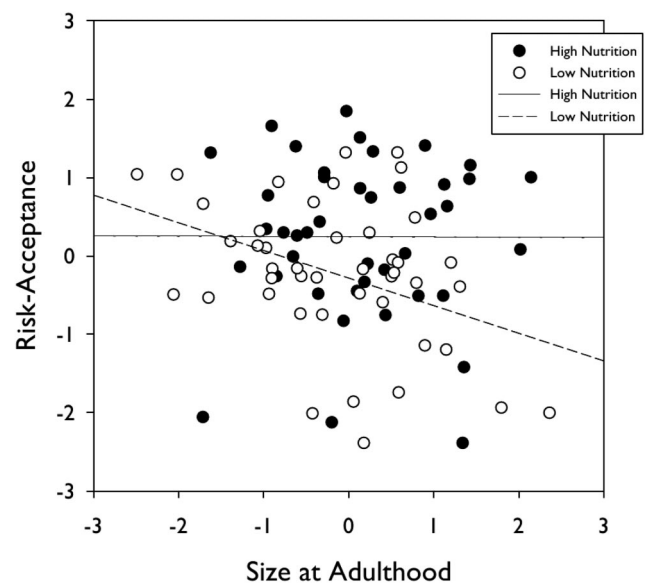


Figure 2. Risk-acceptance as a function of size at adulthood, plotted by nutrition condition during development.

acceptance. Previous research has shown that male redback spiders reared with pheromonal cues simulating dense female populations reached maturity quicker than those individuals not exposed to such cues, and were smaller and in poorer condition in adulthood (Kasumovic & Andrade, 2006). It would be informative to investigate whether such rapid growth is associated with increased risk-acceptance in this spider system.

Aggression

Risk-acceptance has been associated with aggressive behavior in several previous studies, and some have suggested that aggression represents a form of risk-accepting behavior (e.g., Biro & Stamps, 2008; Sih, Bell, Johnson, & Ziemba, 2004). We did not find a relationship between risk-acceptance and aggression in this study. Hissing cockroaches do not appear to experience serious injury in aggressive interactions due to their substantial external armor, and there is a significant large male advantage in winning fights (Clark & Moore, 1995).

Furthermore, male-male aggressive encounters in this species are very common, and almost invariably involve a victor that is clearly determined shortly after any agonistic interaction begins. Agonistic hiss characteristics in hissing cockroaches are correlated with body size, suggesting that honest signaling through hissing may mitigate aggressive encounters between combatants that are highly asymmetrical in size (Clark & Moore, 1995), although this hypothesis has not been tested with playback experiments. Together, these findings suggest that male-male aggression is a relatively low-risk behavior in the hissing cockroach. Risk-acceptance and boldness may be more highly correlated in species where aggressive behavior is associated with high variability in outcome (i.e., aggression carries high costs).

Conclusions

Quality of developmental environment appears to affect risk-acceptance across behavioral contexts in male hissing cockroaches by facilitating condition-dependent risk-acceptance. Our findings contribute to a growing body of research suggesting that risk-acceptance represents an important axis of behavioral variation, and provides some further evidence suggesting that developmental environment plays an important role in facilitating variation in risk-accepting behavior.

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