

Body Size and the Righting Response: A Cost of Reproductive Success in *Nauphoeta cinerea* (Blattodea: Blaberidae)?¹

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Abstract Life history evolution involves a series of trade-offs to maximize reproductive success at the expense of other physiological systems. Within insects, increased body size is associated with increased fecundity in males and females alike; hence, increased body size should be favored even if it is detrimental in the short term. The righting response is a reflexive mechanism used by individuals to regain proper dorsoventral orientation and is conserved among terrestrial animals of multiple taxa to avoid the consequences of being helpless on one's back. In this study, we examined the righting response as it related to body size in the cinereous cockroach, *Nauphoeta cinerea* (Olivier), of both sexes and found that larger individuals were slower to right themselves relative to smaller individuals. Moreover, the reproductive history of the individual at testing differentially affected this relationship in a sex-specific manner. Individual females that were presumed mated at the time of testing were slower to right themselves than were same-sized males, while virgin females righted themselves more quickly. Taken together, these findings suggest that the reproductive gains associated with an increased body size within this species come at the expense of righting ability and that this outcome is compounded by reproductive history.

Key Words righting response, body size, life history, cinereous cockroaches, *Nauphoeta cinerea*

At its simplest, life history theory postulates that organismal fitness is the consequence of a series of physiological and behavioral trade-offs that result in a negative correlation among individual life history traits. This is the consequence of devoting resources toward one process, such as growth or reproduction, at the expense of other processes, such as maintenance (Stearns 1989, Zera and Harshman 2001). Indeed, life history trade-offs have been well documented within multiple species of both vertebrates (Jimenez 2016, Jimenez et al. 2014) and invertebrates (Haag 2013, Ramirez Llodra 2002). They typically involve reduced growth, developmental delays, and/or reduced survival in conjunction with a reciprocal increase in reproductive success and vice versa. Insects have been especially useful for studying the genetic and biochemical bases for these trade-offs with *Drosophila melanogaster* Meigen and the cricket, *Gryllus firmus* Scudder, serving as the dominant models (Bai et al. 2015, Harshman et al. 1999, Rose 1984, Rose and Bradley 1998, Zera and Larsen 2001, Zera and Zhao 2003). Similar

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outcomes have been reported in other species, such as grasshoppers (Hatte et al. 2013), beetles (Trumbo and Robinson 2004, Boman et al. 2008), and cockroaches (Barrett et al. 2009, Jensen et al. 2016, Moore and Sharma 2005). In general, there is a marked relationship between adult body mass and a suite of life history traits within multiple species (Shingleton 2011).

Within insects, body size is an excellent predictor of reproductive capacity (Honek 1993), although environmental factors can impose a high degree of intraspecific variation (Davidowitz 2008). Large females are markedly more fecund than smaller counterparts (Davidowitz 2008, Honek 1993, Jimenez-Perez and Wang 2004, Maxwell and Frinchaboy 2014), while large males enjoy improved mating success. This is the result of increased attractiveness to females and/or increased success during male–male competition (reviewed in Hunt et al. 2009). In addition, within cinereous cockroaches there is a negative correlation between male adult body mass and female gestational period. This effectively increases the number of offspring produced by larger males (Schimpf et al. 2012). As a whole, this suggests there is a selective advantage for large size among individuals of both sexes within cinereous cockroaches and, perhaps, insects in general.

When the legs of an insect lose contact with a substrate, a reflexive righting program (i.e., the righting response) is initiated to restore dorsoventral orientation (Frantsevich 2004 and references therein). Within cockroaches, this response is characterized by dorsal flexion in conjunction with rhythmic bursting of the motor neurons controlling leg movement resulting in a “flailing” motion that allows individual legs to contact the substrate (Camhi 1977, Zill 1986). In an ideal scenario, the forces generated by those legs in contact with the substrate may then be sufficient to cause righting of the animal (Full et al. 1995). Importantly, the righting response is conserved among terrestrial and semiterrestrial species given the myriad situations that could result in an individual being overturned. For example, individuals may fall from an elevated substrate or be turned over due to an aggressive encounter with a conspecific thereby rendering them vulnerable to predation, or simply leaving them stranded and subject to environmental stressors (Golubovic et al. 2013, Penn and Brockman 1995). Indeed, the ability to initiate and complete the righting response has often been cited as an indicator of organismal fitness, but with some caveats (Davy et al. 2014).

Here, we examined the effect of body size on the speed of the righting response within male and female cinereous cockroaches, *Nauphoeta cinerea* (Olivier), with differing reproductive histories. In this study, individuals collected from mass colonies were presumed mated, while individuals maintained as singly housed adults from the day of adult emergence were considered virgins. Despite the fact that some females within this species have the capacity for facultative parthenogenesis (Corley et al. 2001, Moore and Moore 2003), nymphs were never observed in the containers housing individual females used for this study.

Materials and Methods

Insects. Mass colonies were reared in each of two 151-liter (40-gallon) trash barrels with coconut fiber as a substrate and cardboard egg cartons for refugia. Food (Purina Puppy Chow, Nestlé Purina, St. Louis, MO) and a water source

(Fluker's Cricket Quencher with calcium, Fluker's Cricket Farm Inc., Port Allen, LA) were provided ad libitum as needed. An approximately equal number of males and females from each of the two colonies were chosen at random to measure the time to righting as described below.

Meanwhile, cohorts of known age adults were generated via the collection of individual cockroaches directly from the mass colony upon emergence from the final instar. These individuals were identified by the presence of wing buds and/or a white body color at the time of collection. Immediately upon removal, individuals were placed in uniquely identified 1-liter plastic containers with coconut fiber and an aluminum weigh dish to serve as both a watering tray (Cricket Quencher as above) and a refugium for individual cockroaches. Food (Puppy Chow) and water were provided ad libitum as needed. Initially, the lighting and temperature regimen was not fixed, but each colony and the individual roach habitats were moved to an environment with a fixed 12:12 light:dark lighting regimen and maintained at 22°C for at least 1 mo prior to testing.

Righting response. The protocol used was similar to that of Ridgel et al. (2003). In brief, individual cockroaches were removed directly from either the mass colonies or their individual holding containers and placed on their backs in a 17.5-cm \times 15.5-cm \times 7.5-cm plastic container. The container was lined with a 2-cm-thick Styrofoam block, which left 5.5 cm from the Styrofoam surface to the top of the container. Each roach was briefly (<1 s) on its back, then released with timing beginning immediately upon release. Timing stopped once the cockroach successfully righted itself. All times were recorded to the nearest hundredth of a second. In instances where an individual failed to right itself within 30 s ($<2\%$ of all trials), the trial was stopped and the time was recorded as 30 s for statistical purposes. Individuals sampled from the mass colonies ($n = 364$) were tested a single time while individuals from the known-age cohorts ($n = 124$) were tested three consecutive times with a 15–30-s rest period between trials. At the time of testing, these individuals were between 1 and 13 mo of age. Prior to analysis, the time-to-righting data for each sex and colony condition (by cohort) were transformed via a Box–Cox procedure to ensure normality (Box and Cox 1964). All statistical analyses were conducted using NCSS11 (NCSS Statistical Software, Kaysville, UT).

Immediately after testing, individual cockroaches were anesthetized using cold (0–4°C) for 5 min then weighed to the nearest hundredth of a gram followed by the estimation of the total body length (tip of head to tip of abdomen) to the nearest millimeter. In addition, a simple index of relative body size was calculated for individual cockroaches using the ratio of their body mass (in grams) to their body length (in millimeters). Those individuals with a higher body size index are relatively heavy for their length, but this measure is not meant to be reflective of body condition per se.

Results

Female cinereous cockroaches were significantly heavier than their male counterparts, regardless of the colony condition (two-sample t test, $P < 0.04$ for all). They also tended to be longer, although this difference was not always significant. Finally, we found that the body size index of the females was always

Table 1. Body length, body mass and body size index (mean \pm SEM) for male and female cinereous cockroaches of either mixed (mass colony) or known age (cohorts). *P* values indicate statistical significance after two-sample *t* test.

Group	Age at Test (mo)	Mass (g)	Length (cm)	Index ([Mass/Length] \times 100)
Mass colony	N/A			
Females (n = 171)		0.68 \pm 0.01	2.95 \pm 0.02	23.03 \pm 0.2
Males (n = 193)		0.51 \pm 0.01	2.67 \pm 0.01	19.08 \pm 0.19
<i>P</i> value		<0.001	<0.001	<0.001
Cohorts				
Cohort 1	1.0–1.6			
Females (n = 26)		0.63 \pm 0.02	2.74 \pm 0.04	22.83 \pm 0.61
Males (n = 17)		0.53 \pm 0.02	2.70 \pm 0.04	19.48 \pm 0.75
<i>P</i> value		0.03	0.98	0.01
Cohort 2	4.9–5.5			
Females (n = 27)		0.68 \pm 0.02	2.84 \pm 0.03	23.84 \pm 0.60
Males (n = 12)		0.57 \pm 0.03	2.73 \pm 0.05	20.87 \pm 0.90
<i>P</i> value		0.03	0.53	0.07
Cohort 3	11.4–12.2			
Females (n = 21)		0.72 \pm 0.02	2.87 \pm 0.04	25.09 \pm 0.68
Males (n = 22)		0.62 \pm 0.02	2.82 \pm 0.04	21.81 \pm 0.66
<i>P</i> value		0.01	0.97	0.01

significantly greater than that of the males (two-sample *t* test, $P \leq 0.01$) with the exception of those individuals from Cohort 2 (Table 1).

Two-way analysis of variance indicated a significant effect of both age (cohort) and sex on righting time in the known-age individuals. In particular, there was a significant main effect of age for each of the three morphological measures (body mass, body length, and body size index; $P < 0.01$ for all); older individuals were significantly larger. There was also a significant main effect of sex for body mass and body size index only ($P < 0.001$) in that female cockroaches were larger than males. The main effect of sex on body length was not statistically significant ($P = 0.058$). The cohort \times sex interaction term was also not significant for any comparison ($P > 0.6$) (Table 2).

Interestingly, the reproductive history of individual cockroaches modulated this response in a sex-specific manner. In particular, the righting time of female

Table 2. Effect of age (cohort) and sex on body mass, body length, and body size index in virgin cinereous cockroaches. A full-factorial two-way analysis of variance was constructed separately for each measure.

Measure	Factor	df	<i>F</i>	<i>P</i> Value
Body mass	Cohort	2	8.07	0.001
	Sex	1	30.36	<0.001
	Cohort \times sex	2	0.04	0.96
	Error	119		
Body length	Cohort	2	4.87	0.01
	Sex	1	3.66	0.06
	Cohort \times sex	2	0.37	0.69
	Error	119		
Body size index	Cohort	2	5.72	0.004
	Sex	1	30.67	<0.001
	Cohort \times sex	2	0.04	0.96
	Error	119		

cockroaches from the mass colonies was slower than that of similarly housed males, while the opposite was true for singly housed individuals of known age. In other words, the righting times of females from the mass colonies were slower than that of males raised under identical conditions per unit of measure. On the other hand, singly housed males had a slower righting time than singly housed females per unit of measure (Fig. 1). Unfortunately, the relatively small sample sizes ($n = 12$ to 27) precluded performing these analyses within the individual cohorts.

In the group-housed insects, an analysis of covariance (ANCOVA) indicated that the effect of body length, body mass, and body size index was significant for each measure ($P < 0.001$), as well as the effect of sex ($P < 0.001$). Meanwhile, in singly housed individuals, ANCOVA indicated a significant effect of only body mass, body size index, and sex on individual righting times ($P \leq 0.01$ for all); body length had no effect on righting time. Although the specific reproductive history of individuals sampled from the mass colony was unknown, they were presumed to have mated while the singly housed individuals were never in the presence of the opposite sex posteclosion. Since individuals of this species are not reproductively mature until at least 6 d old (Corley et al. 2001, Moore and Moore 2003), it is reasonable to assume that singly housed cockroaches were virgins at the time of testing.

Lastly, it appeared there was a significant effect of age (cohort) at the time of testing on the righting time within the singly housed individuals (data not shown). However, given that body length, body mass, and the body size index were greater as the age of the individuals increased regardless of sex (Table 1), we chose to reevaluate the effect of age on righting time after adjusting for the age-specific

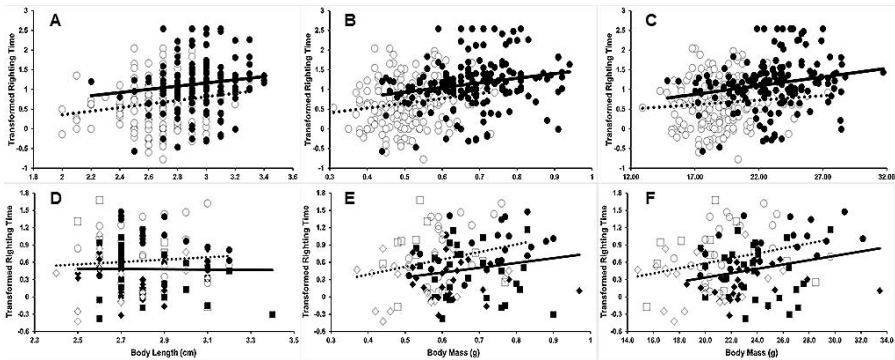


Fig. 1. The relationship between each morphological measure and the time to righting within group-housed, mated individuals (A–C) and singly housed virgin individuals (D–F). Each point represents the time to righting for individual cockroaches. Closed symbols represent the values for females while the open symbols represent the values for males. Lines indicate the best-fit regression for each measure within individual sexes (females = solid lines; males = dashed lines). In D–F, individual shapes represent the age (cohort) at time of testing (\diamond , Cohort 1; \square , Cohort 2; and \circ , Cohort 3). Individual sample sizes ranged from 12 to 191 within each sex and/or cohort. See text for details regarding statistical analysis.

variation in each of these measures. In brief, the relationship between the residuals of the righting time (after adjustment for age) and each of the morphological measures (also after adjustment for age) was assessed using simple linear regression (as in Speakman 2005). For both males ($P \geq 0.35$) and females ($P \geq 0.13$), the apparent effect of age on righting time was not observed after this adjustment (not shown).

Discussion

Despite its use as an indicator of fitness in vertebrates (Davy et al. 2014), the righting response remains underutilized within invertebrates. Our data indicate that simple morphological measures are correlated with the ability of cinereous cockroaches to right themselves under controlled conditions, and that larger individuals were slower to right themselves (Fig. 1). This relationship may reflect a trade-off between body size and reproduction given that the reproductive success of larger individuals of both sexes is greater and, taken together, these data suggest that increased fecundity may come at a cost. In addition, we found the presumed reproductive history of the individuals further modulated this response or, more specifically, that virgin females were quicker to right themselves on a per-unit-of-measure basis relative to virgin males while the opposite was true for individuals that were presumed to be mated (Fig. 1).

In general, we found that individual body mass, as well as the individual body size indices, were the best predictors of the righting time in each sex regardless of the insect condition. Presumably, this reflects the need to generate more force at the time the leg contacts the substrate for larger individuals to right themselves. Moreover, given the righting response in cockroaches relies on a standardized, yet somewhat uncoordinated, flailing of the legs, the longer time to righting may be a consequence of chance (Full et al. 1995). That is, it may simply require more time for the legs to contact the substrate “just right” in order to generate the force needed for larger individuals to right themselves (Faisal and Matheson 2001). Meanwhile, the lack of a relationship between body length and the righting time of individual cockroaches is likely the consequence of their body plan. In particular, cockroaches have broad, flattened bodies in conjunction with relatively short legs; hence, the total length of the individual is unlikely to influence the likelihood of the tarsi contacting the substrate (Faisal and Matheson 2001). Since we did not collect any measures of either body (e.g., pronotum) width or leg (e.g., femur) length, we are unable to determine whether these measures are important determinants of righting times within this species.

Overall, the relationship between morphological measures and the righting response has gone largely unexplored in both vertebrates and invertebrates. Instead, the emphasis has centered largely on deducing the developmental effects of various environmental factors, and their subsequent impact on measures of locomotor ability, including righting times. Not surprisingly, developmental derangements often have an adverse effect on the righting response within multiple species (Farkas et al. 2009, Hurst et al. 2014, Sim et al. 2015).

As with any organism exhibiting determinant growth, the final body size of cockroaches at adulthood is a fixed trait, and this is especially true for linear measures such as body length. Hence, we believe the apparent age-related increase in both body mass and body length in our singly raised adult population is an artifact of changes in housing conditions with time (Table 2). In particular, known-age individuals used in this study were collected directly from the mass colonies at approximately 5–6-mo intervals; however, these colonies were maintained in the absence of active population control. Consequently, the density within each colony notably increased with time, thereby reducing resource availability to the developing immatures in the younger cohorts. The detrimental effect of resource limitation on growth rates and final body size is well known (Abrams et al. 1996, Dmitriew 2011). Importantly, after accounting for the age (cohort)-specific variation (Table 1), we found no effect of aging on righting times in cinereous cockroaches. This lack of an effect on righting times is consistent with a previous study examining aging and locomotor behavior in other species of cockroaches (Ridgel et al. 2003).

Given that larger individuals of both sexes were slower to right themselves, and that larger individuals within insects typically enjoy increased reproductive success, these data suggest that body size variation may represent a life history trade-off within cinereous cockroaches or, more specifically, that increased reproductive success associated with larger body sizes comes at a risk. In particular, there is an increased likelihood of mortality should a large individual become overturned relative to a smaller individual. Although the degree to which this happens in nature

is unknown, we commonly see individual cockroaches on their backs within the group-housed laboratory populations (J.M.H. pers. obs.).

Furthermore, since female cinereous cockroaches are ovoviviparous, a substantial proportion of their adult body mass is attributable to the presence of mature ovarioles and/or ootheca within mated individuals. More interestingly, resource limitation within this species is actually associated with an increase, not a decrease, in female fecundity (Barrett et al. 2009). Consequently, the largest females from the mass colonies should enjoy the greatest reproductive success despite having the slowest righting response on per-unit measures of body mass, body length, or body size index. Meanwhile, the largest singly housed males should have the greatest potential for reproductive success if given the opportunity, even if they are slower to right themselves on a per-unit basis. Further support for this idea is provided by the occurrence of oosorption within unmated females of this species (Barrett et al. 2009). This would reduce the burden associated with reproductive organ size in unmated females.

Ultimately, these data were collected with the goal to determine whether aging had an effect on the righting response within this species, as well as whether the effect of age varied with sex. They were not collected to address hypotheses concerning differences in body size among individual cockroaches and their effects on the righting response. It was only during preliminary analyses that the specific relationship between morphological measures and righting times was observed, as well as the sex-dependent variation in the speed of the response. This led us to expand our initial dataset to include individuals from each of the reproductive conditions to corroborate, or refute, our initial findings. Unfortunately, this means meaningful data, for example additional morphometric measures or fecundity data from tested individuals, are lacking. Nonetheless, we believe they make a compelling argument for an unappreciated role of body size and reproductive history on life history trade-offs within cockroaches.

In conclusion, we found that body size, and especially body mass, has a significant effect on the righting ability of both sexes of the cinereous cockroach. Larger individuals, which are typically more fecund, are slower to right themselves. In addition, our data suggest that reproductive history further modulates this response in a sex-specific manner or, more specifically, that mated females are slower to right themselves relative to same-sized males while virgin females are quicker to right themselves relative to same-sized virgin males. Presumably, this is a reflection of the burdens imposed by the increased weight of the maturing ovarioles and/or the developing brood within the mated females of this ovoviviparous species.

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