

Sexual Conflict and the Energetic Costs of Mating and Mate Choice in Water Striders

Paul J. Watson,^{1,*} Goran Arnqvist,^{2,†} and Robert R. Stallmann^{1,‡}

1. Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131-1091;

2. Department of Animal Ecology, University of Umea, S-901 87 Umea, Sweden

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ABSTRACT: Analyses of intersexual conflicts of interest over courtship, mating, or mate guarding require an understanding of the physiological costs of sexual interaction. Repeated respirometric measures of energetic expenditure were taken on female *Aquarius remigis* while unladen and while carrying a mating male, a small metal weight, or a euthanized male. Unladen "cruising" locomotion consumed an average of 334.6 μW of energy ($82 \text{ J kg}^{-1} \text{ m}^{-1}$); this estimate of the cost of locomotion coincides with measures from voluntarily locomoting arthropods of similar mass and represents the first energetic measure of skating on a water surface. Cruising females carrying males or metal weights consumed 24% and 28% more energy than unladen females, respectively. Females engaged in "escape" locomotion consumed 43% more energy while carrying a male than while unladen. Further, our study shows that premating struggles, and therefore selective mating decisions, are energetically costly. Struggling females consumed an average of 936.6 μW , a 126% increase compared to cruising, non-struggling females, and 64% more than mating females engaged in escape locomotion. We develop a quantitative model showing that at a certain harassment rate threshold, accepting superfluous matings becomes the "best of a bad job" for females.

Keywords: sexual conflict, energetics, mate choice, respirometry, Gerridae.

For many sexual organisms the pivotal reproductive event of fertilization is nested within a labyrinth of male and female mating behaviors, each entailing certain costs and benefits. While much research has been devoted to

assessing the benefits of alternative male and female mating behaviors, there is good reason to place more effort into measuring the costs associated with these behavioral options. The costs and benefits involved in various reproductive decisions are typically asymmetric for males and females, leading to sexual conflict. Current mating system theory focuses on these conflicts. Mating systems are viewed as evolutionarily dynamic resolutions of sexual conflicts of interest (e.g., Magurran and Nowak 1991; Gowaty 1994; Magurran and Seghers 1994; Rowe et al. 1994; Clutton-Brock and Parker 1995; Alexander et al. 1997; Choe and Crespi 1997). Mating systems are usually characterized by enough residual intersexual tension and behavioral options that each individual's selection of tactics for profiting more from a given interaction, while paying less, directly affects each participant's fitness. Sexual conflict is thus at the heart of evolutionary ecology. As stressed by Parker (1979, 1984), however, a clear demonstration of sexual conflict requires a quantitative assessment of the potential costs involved for both sexes. Such assessments are often difficult to perform empirically (e.g., see Lauer et al. 1996) and, thus, are rarely made despite their theoretical importance (Arnqvist 1989; Watson 1993).

Costs of various components of mating, such as male display behavior or female coyness, are key considerations in most models of sexual selection, since some form of evolutionary "balance" between benefits and costs is assumed (Andersson 1994). Again, despite their critical importance for testing sexual selection models, few studies have made quantitative estimates of the costs of sexual behaviors or traits (Partridge and Endler 1987; Arnqvist 1994; Watson and Lighton 1994). In models of sexual selection by female choice, costs of mating and mate assessment alter optimal mate choice behavior (Parker 1983; Real 1990, 1991; Crowley et al. 1991; Andersson 1994; Dombrowsky and Perrin 1994). Some empirical studies also show changes in mate choice when females' mating costs are manipulated (Arnqvist 1992; Forsgren 1992; Rowe 1994). Thus, a lack of understanding of the costs of mating associated with specific social

* To whom correspondence should be sent; E-mail: pwatson@unm.edu.

† E-mail: Goran.Arnqvist@animacol.umu.se.

‡ E-mail: bstall@unm.edu.

or ecological contexts may lead to an impression that much female mating behavior is arbitrary and capricious when in fact it is tuned to make the best of the prevailing environmental conditions.

The potential costs of mating to females include time devoted to mating (Martens and Rehfeldt 1989), energetic costs of reproductive behaviors, increased risk of predation while mating (Gwynne 1989; Magnhagen 1991; Arnqvist 1997), risk of disease or parasite transmission, and risk of death or injury inflicted by the male (Daly 1978; Parker 1979; Le Boeuf and Mesnick 1991; Ward et al. 1992). While a great deal of attention has been paid to measuring costs arising from an increased risk of predation during mating (Gwynne 1989; Magnhagen 1991), other cost components have received less attention (Andersson 1994). Time and energy costs of mating are no doubt the most general of all costs (Daly 1978), but detailed studies of the energetics of mating are nevertheless few and often incomplete (Halliday 1987). Energetic costs of mating may arise from direct metabolic costs of sexual behaviors (e.g., production of vocal, visual, chemical, tactile, or vibratory signals; Halliday 1987; Watson and Lighton 1994), costs of production of gametes and nutritious accessory substances (Halliday 1987; Gwynne 1997), increased metabolic costs expended on general nonsexual activity during mating (e.g., locomotion), and reduced foraging efficiency (Robinson and Doyle 1985; Magurran and Seghers 1994; Jormalainen and Merilaita 1995; Stone 1995).

In a wide range of arthropod taxa, mating involves male-female associations beyond the time required for sperm transfer (Ridley 1983; Alcock 1994). During these pre- and postcopulatory guarding phases, the female typically carries the male, often for long periods. Robinson and Doyle (1985) showed that such pairing interfered with foraging in amphipods and, in this sense, entailed energetic costs. However, to our knowledge, no study has addressed the most general potential energetic cost involved: increased metabolic expenditure for females when transporting passive males during mating.

The costs and benefits of mating are relatively well studied in water striders (see Rowe et al. 1994; Arnqvist 1997), and this group of insects has become a model system for the study of sexual conflicts and mating system evolution. In most species, the basic mating scheme can be described as follows (Rowe et al. 1994; Spence and Andersen 1994; Arnqvist 1997). Matings are initiated by males who lunge at and attempt to grasp females. Females are typically reluctant to mate, and thus try to dislodge males by struggling vigorously (Arnqvist 1992; Lauer et al. 1996). If the male can subdue the female, copulation follows. Matings are prolonged beyond the time required for sperm transfer due to a guarding pe-

riod of variable duration (from a few minutes up to several weeks) where the male rides passively on the back of the female. During this postcopulatory guarding period, the female is responsible for all locomotory activity of the pair. Matings are usually ended with a postmating struggle initiated by the female. Both sexes multiply mate.

Matings are costly to female striders in terms of an increased risk of predation (Arnqvist 1989; Fairbairn 1993; Rowe 1994) and a reduced mobility when carrying males (Arnqvist 1989; Fairbairn 1993). Despite the reduced mobility, short-term foraging success is not necessarily reduced by mating, since foraging is not interfered with by male harassment as frequently for mating females as for single females (Wilcox 1984; Fairbairn 1993; Rowe et al. 1996). However, to determine the net energetic costs of mating for females, energetic expenditures must be studied: maintaining a certain level of foraging success is likely to come at a higher energetic cost to mating females, since females carrying passive males are likely to expend more energy per time unit (or per distance traveled) compared with single females (Arnqvist 1997). In accordance, Fairbairn (1993) found a tendency for females carrying weights (mimicking the weight of a male) to accumulate less lipid compared with unladen females. In the current study, we employ CO₂ respirometry to measure directly the energetic costs of mate-carrying and mate-rejection behaviors in the water strider *Aquarius remigis* (Heteroptera; Gerridae).

Methods

Animal Care

Male and female *Aquarius remigis* were collected on March 19, 1995, from a wingless, reproductively active population in Water Canyon in the Magdalena mountains of central New Mexico. In the lab, the sexes were separated and kept in glass aquariums with 10 cm of clean aerated water. All individuals were marked for individual identification. Evaporated water was replaced with distilled water, and the tanks were entirely cleaned at 2-wk intervals. The striders were fed an ad lib. diet of live-frozen early instar crickets. Styrofoam floats provided resting and oviposition sites. After a period of preliminary data collection during which we adjusted our techniques, we combined the sexes in each aquarium, providing an even sex ratio and a density of approximately 74 striders m⁻² of water surface.

Respirometry

Gas exchange data were collected using an Ametek S3A-II O₂ analyzer and Licor LI-6251 CO₂ analyzer connected

in series in a Sable Systems TR-3 flow-through respirometry system (Sable Systems, Henderson, Nev.). Our methodology allowed continuous recording of gas exchange with a temporal resolution of approximately 2 s.

The respirometry flask had a total volume of 270 mL. With 50 mL of water in the flask, the circular water surface available for the striders was 10 cm in diameter (approximately 78.5 cm² in area). There was 3.5 cm of “headroom” for the striders between the water surface and the chamber’s ceiling. The water was set in motion by a wire stir-bar rotating at approximately 100 revolutions min⁻¹, producing a standard current at the surface that required the strider to make a swimming stroke about once per second to maintain its position in the flask. The surface current was estimated to be 418.7 cm min⁻¹ by determining the rotational speed of a floating stick and multiplying by the circumference of a circle with 0.75 the flask’s radius, the distance from the flask’s center at which striders typically spent most of their time.

In nature, *A. remigis* forages on moving water by maintaining a position on the stream and waiting for dead arthropods floating on the surface to be washed into their foraging area. Thus, unlike most insects, *A. remigis* is adapted for “treadmill locomotion” on turbulent waters. However, the rather unnatural rotational movement of the water in the respirometry flask may not have yielded ideally representative estimates of the cost of locomotion. Moreover, the locomotion induced by our circular aquatic treadmill, while not “forced” to the same degree as by the terrestrial treadmills often used in energetics studies (i.e., a strider that does not locomote simply rotates slowly in the flask instead of being continuously jammed against a wall) still cannot fairly be called completely voluntary, because in nature striders are averse to drifting for more than a few seconds on moving water. Thus, absolute values of locomotor costs are presented as tentative estimates, and we focus rather on the differences in costs for laden and unladen females, as well as on the costs of premating struggles.

The rotating water in the respirometry flask did not cause inaccuracies in our data. Although the CO₂ analyzer is sensitive to water vapor, the passage of initially dry air through the flask at our flow rate of 375 mL min⁻¹ resulted in air that was still quite dry passing to the analyzer. Preliminary trials without water striders, in which we compared the performance characteristics of the respirometry system with and without 50 mL of rotating water in the respirometry flask, showed that equilibrated CO₂-free water did not absorb detectable amounts of introduced CO₂ at our flow rate. We determined this by performing repeated injections of 0.4 mL of fresh air into the scrubbed airstream entering the flask ($N = 23$

injections into the flask with stirring CO₂-free water and 14 injections into a completely dry flask) and calculating the area under each spike in the analyzer’s output. These 0.4 mL injections caused response spikes of a size comparable to those typical of a relatively small increase in the CO₂ output of a water strider if, for example, the strider changed from a resting state to one of relaxed locomotion. Mean areas were 25.48 (SD = 7.14) for the dry flask versus 23.66 (SD = 8.08) for the wet flask (separate variances $t = 0.713$; $df = 30.3$; $P = .48$). Moreover, there was no discernable blunting of the system’s response to these injections in the wet versus dry flasks. Finally, once the flask containing water had equilibrated (after about 30 min at a flow rate of 375 mL min⁻¹) the baseline output was nearly as stable as for a dry flask. Thus, we zeroed the CO₂ analyzer and performed corrections for baseline drift using data from the flask with stirring water but without a water strider present.

Temperatures in the respirometry chamber varied between 21.7° and 31.1°C ($\bar{X} = 25.8$; $SD = 2.09$) across all recordings. Temperatures rarely varied more than 3°–4°C during any one recording period (SD within recordings averaged 0.61°C).

Data Collection

The locomotory and sexual behavior were observed continuously throughout respirometric recording (see appendix for behavior definitions). Sable Systems Datacan V real-time data acquisition software allowed incorporation of behavior codes directly into the respirometric record. Using a stopwatch set to beep each minute, we also made summaries of the duration and intensity of locomotion for each minute of recording on paper forms, classifying the locomotion as either cruising or escape and as having occurred for ≤ 20 s, ≤ 40 s, or for the entire minute (striders sometimes gripped the flask wall with one to two legs and rested on the moving water). When possible, the percentage of escape versus cruising locomotion within a minute was also noted. We also counted the number of struggling acts that occurred each minute. Sample sizes for each kind of behavior for which we have estimated energy costs are given in table 1.

We initiated most trials by selecting a pair of striders already in the mating position and transferring them with flexible insect forceps into the respirometry flask. Nearly all pairs continued mating after this brief handling. To speed equilibration of the atmosphere in the flask after transfer of the striders, we purged the CO₂ from the water beforehand via 30–40 min exposure to a CO₂-free 375 mL min⁻¹ airstream while the water was continuously stirred. The stirrer was turned off and the water exposed to ambient CO₂ only for 2–3 s during the

Table 1: The number of separate recording sessions, number of different subjects, and the total minutes of recording for estimates of the energy use during various behaviors

<i>Behavioral context and subjects</i>	<i>Number of records*</i>	<i>Number of subjects†</i>	<i>Minutes of recording</i>
Stationary:			
Solitary female	5	5	20.7
Solitary male	27	22	163.6
Mating pair	8	8	82.5
Nonmating pair	11	8	92.7
Cruising locomotion:			
Solitary female	34	29	246.4
Mating pair	30	27	409.9
Weighted female	20	19	209.8
Female with dead male	16	15	151.0
Solitary male	5	5	19.1
Escape locomotion:			
Solitary female	15	11	130.7
Mating pair	7	7	112.7
Weighted female	9	7	65.3
Female with dead male	5	5	46.2
Struggling pairs:			
Struggling	12	8	98.7
Mating (control)	12	8	168.6

* The number of recording sessions providing respirometric data in the given context.

† The number of different females (for records involving pairs or solitary females) or males (for data on solitary males) providing respirometric data within the given context.

transfer, after which the flask was quickly returned to a CO₂-free state using the same flow rate.

Repeated measures of energetic costs of cruising locomotion under two to four treatment conditions were obtained from a number of females (table 1). These data were gathered using the following sequential protocol. A mating male/female pair was selected from a holding tank and placed in the respirometer. We began obtaining energetic data at cruising speed for the mating female. Twenty to 30 min usually were required to obtain a flat recording of CO₂ output during consistent cruising locomotion. The pair was then separated and a solder weight was attached to the dorsal surface of the female's thorax using double-sided tape. The solitary male's standard metabolic rate (SMR: the temperature-adjusted "resting" metabolic rate) was measured while the solder-laden female rested alone in a holding tank. After measuring the male's SMR, the male was euthanized in ethyl acetate. We then placed the weighted female alone in the respirometer and again recorded her cruising-speed energy consumption. Finally, we removed the solder weight from the female, attached the euthanized male, and again recorded the energy use of the female while cruising. Males and females were weighed live to the nearest 0.1 mg (immediately after the mating-pair recording) using

a Mettler AC88 digital balance. Females were reweighed after application of the weight and the dead male. If females were injured in handling or appeared to become exhausted at any stage (e.g., if they drifted more than usual) they were not included in the final data analyses. Because of the consequent unequal samples in each treatment, the repeated measures were compared using paired *t*-tests rather than repeated measures ANOVA.

Data Analysis

Respiratory Exchange Ratios. For conversion of VCO₂ (i.e., the volume of CO₂) to VO₂ and energy, the respiratory quotients (RQ: the ratio of CO₂ produced to O₂ consumed) of six females were determined. Female *A. remigis* were collected in mid-October 1994 from a healthy, reproductively active population in the vicinity of Albuquerque, N.M. These individuals were tested on October 26. They were kept for several days under the same lab conditions and fed the same food (frozen adult *Drosophila* fruitflies and early instar *Gryllus* crickets) before testing as the individuals used in the energetic studies had been. Each female was kept for 3.5 h in a sealed 20-mL syringe at 22.6°–23.3°C, thus allowing a cumulative, partial depletion of O₂ and addition of CO₂. The females en-

gaged in periodic locomotory behavior in the syringes, but it is unlikely that they were active enough to cause departures from steady state metabolism (i.e., where O_2 enters the animal at the same rate that it is consumed and CO_2 leaves the animal at the same rate that it is produced). After the waiting period, 10 mL of the partially respired air inside each syringe was injected through self-sealing PharMed tubing into a dry CO_2 -free airstream flowing at 100 mL min^{-1} . We waited for the system to return to baseline conditions between injections. Before and after the series of six females, an atmospheric control sample was injected to measure the amount of CO_2 in the air originally supplied to the females in the syringes. Individual RQs were calculated from the O_2 and CO_2 response areas for each injection by the standard formula $(CO_2 \text{ animal} - CO_2 \text{ control}) / (O_2 \text{ animal} / 1 - 0.2095)$. The resulting RQs ranged from 0.81 to 1.07, and the average RQ of 0.972 (SD = 0.084) was used in data conversions.

Data Conversions. All data adjustments and conversions were performed using Datacan V analysis software from Sable Systems. Level baseline readings were taken on CO_2 -free airstreams at the beginning, end, and sometimes in the middle of each recording. Baseline data were collected from the same flask, including water and stir speed used during the associated strider recordings. Before data conversions, we used linear baseline correction to adjust for small shifts in the zero reading of the CO_2 analyzer within each recording. Raw parts per million of CO_2 data were then converted to V_{CO_2} . These data were smoothed and temperature data were used to adjust V_{CO_2} to a standard of 25°C using a Q_{10} of 2.0. The data then were converted to Vo_2 using the empirically determined RQ and finally converted from Vo_2 to joules (J) or microwatts ($\mu\text{W} = \mu\text{J s}^{-1}$).

Results

Standard Metabolic Rate

Observed standard or “resting” metabolic rates (SMR) ranged from 0.80 to $3.61 \mu\text{W mg}^{-1}$ for males ($\bar{X} = 2.21$, SEM = 0.15, $N = 27$) and from 0.99 to $2.04 \mu\text{W mg}^{-1}$ for females ($\bar{X} = 1.41$, SEM = 0.19, $N = 5$). The average masses of males and females in this sample were 42.3 mg (range = 32.5–51.7, $N = 27$) and 54.1 mg (range = 47.6–63.7, $N = 5$), respectively. The SMR in microwatts scaled to body mass in mg (m) at 25°C , according to the equations:

$$\text{SMR}_{\text{male}} = 36.16 \cdot m^{0.253} \quad (1)$$

and

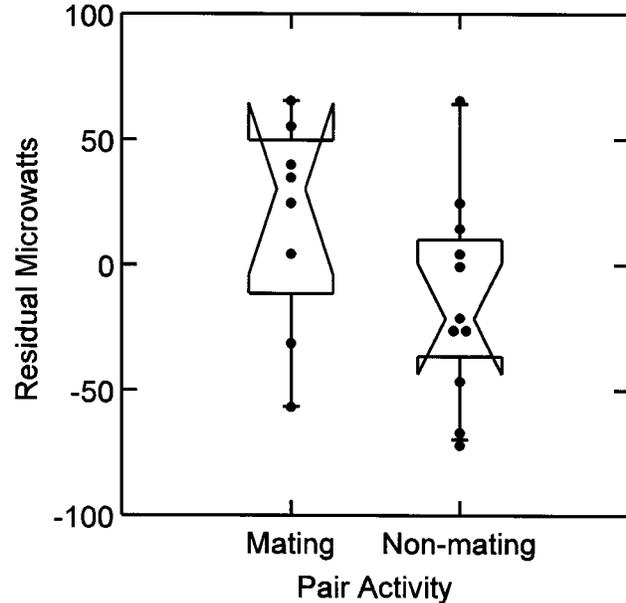


Figure 1: Combined resting metabolic rates of *Aquarius remigis* pairs while mating ($N = 8$) or not mating ($N = 11$). Residual microwatts (Y-axis) are residuals of the linear regression of the summed male and female metabolic rates versus the summed body mass of the male and female. Dots show actual values of data points. The box plots mark the median at the center of the constriction and 95% confidence intervals by the extent of the constrictions. Upper and lower horizontal lines (box edges) show the upper and lower quartiles and the whisker ends show the most extreme values falling within 1.5 times the interquartile range of the upper and lower quartiles. Metabolic rates are standardized for temperature (ca. 25°C).

$$\text{SMR}_{\text{female}} = 47.85 \cdot m^{0.114}. \quad (2)$$

The male and female equations do not differ significantly (parameter: asymptotic standard error ratios were 0.76 and 0.72 for β_0 and β_1 of the male equation, respectively, and only 0.22 and 0.10 for the female equation).

Energetic Cost of Mating

Nonlocomoting pairs of striders consumed slightly more energy in the mating position than when the male was standing on the water surface out of contact with the female (fig. 1); the difference is marginal when comparing residuals adjusted for each pair’s body mass (Mann-Whitney: $\chi^2 = 2.73$, df = 1, one-tailed $P = .054$; exact P value, robust to small sample size). On average, stationary pairs in the mating position consumed $33.2 \mu\text{W}$ more energy than nonmating pairs—a 25% increase (using least-squares means adjusted for each pair’s body mass).

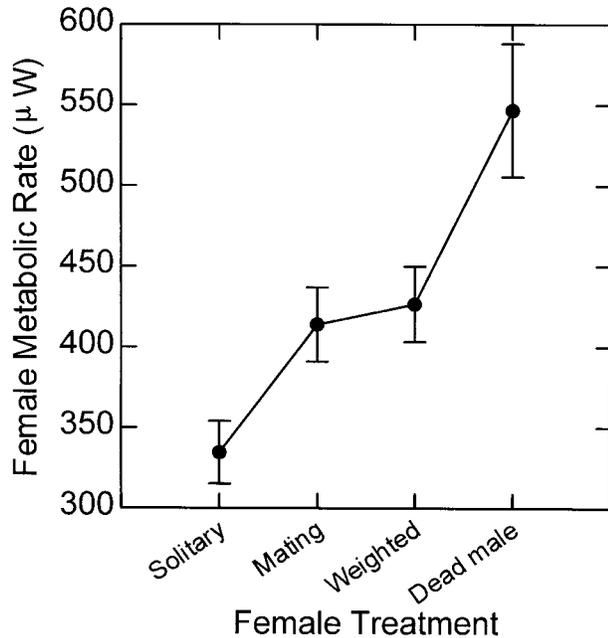


Figure 2: Energy expenditure by females engaged in consistent cruising locomotion during four different female treatments: solitary, mating (mounted male with genitalia attached or unattached), carrying a lead weight, and carrying a dead male in the mating position (same male as carried in treatment 1). The figure shows means (± 1 SEM) for all the data collected; sample sizes for statistical analyses are smaller because only paired data were used to contrast treatments (i.e., repeated measures of the same female during a single 90–120-min trial period).

Comparative Energetic Costs of Locomotion

Cruising Locomotion. Solitary females that were engaged in consistent “cruising” locomotion consumed, on average, 334.6 μW of energy ($5.7 \mu\text{W mg}^{-1}$, average mass = 59.7 mg). Given the speed of water movement in the flask of $418.7 \text{ cm min}^{-1}$ (at 0.75 the flask’s radius), this amounts to a routine gross cost of body carriage (i.e., positional maintenance on the circular water current) of $82 \text{ J kg}^{-1} \text{ m}^{-1}$ ($= 4.1 \text{ mL O}_2 \text{ kg}^{-1} \text{ m}^{-1}$) during locomotion. The slope of the simple regression line connecting mean female SMR (speed = 0) and mean metabolic rate (MR) during cruising without a load at our single imposed speed suggests that each meter per minute increase in speed requires an additional $61.9 \mu\text{W}$ of energy consumption by the female.

Mating females, weighted females, and females carrying a dead male all used significantly more energy to maintain cruising behavior than did unladen solitary females (fig. 2; three contrasts using paired t -tests: $N = 27$, 20, and 16, respectively, all $P < .007$). Comparing treatment means based on all the females we measured, cruis-

ing females carrying males used $413.9 \mu\text{W}$ of energy (SEM = 23.0, $N = 30$) and females bearing solder weights used $426.5 \mu\text{W}$ (SEM = 23.3, $N = 20$)—23.7% and 27.5% more energy, respectively—than females cruising without a load. The increase in energy consumption by weighted females over those with a live male may have been due to the higher average mass of the solder weights compared with that of live mating males (55.5 mg, mean load ratio = 1.95 for the solder weights vs. 42.9 mg, mean load ratio = 1.73 for males; load ratio = laden female mass/unladen female mass). The estimated cost of carrying euthanized males ($N = 16$) was higher still: 63.4% above that incurred by solitary cruising females. The relatively high energy use when loaded with the euthanized male might be partly due to some of his legs dangling in the water or rubbing against the female’s legs.

We compared the efficiency with which females can carry a load versus their own body mass using an ANOVA with female MR as the dependent variable and two independent variables—the summed male and female body mass and a variable indicating whether the female was unladen, carrying a live male, or carrying a solder weight—as well as an interaction term. Total mass had a significant effect on female MR ($F = 4.25$, $P = .041$), increasing female energy consumption by $6.9 \mu\text{W}$ for each additional milligram of weight. The type of load and the mass-by-load interaction were not significant predictors of MR ($F = 0.43$, $P = .62$ and $F = 0.58$, $P = .56$, respectively), showing that the unit cost of load was indistinguishable from that of own body carriage (fig. 3).

Although cruising while carrying a male clearly costs females more than cruising without a male, our data provide no evidence of strong natural selection for reduced male size to ameliorate the female’s cost of transport. Within the range of male body mass that we utilized, and controlling for female mass, there was not a significant relationship between female energy consumption and male mass (partial $r = 0.01$, $N = 30$, $P = .95$). Natural selection also seems not to be favoring increased female size to reduce the cost of carrying males. With male weight held constant and estimated male and female SMR subtracted from total MR records of mating cruising pairs, larger females actually used more energy (partial $r = 0.46$, $N = 30$, $P = .013$). Inclusion of a male-by-female body mass interaction term in the model indicated that the unit cost of carrying males was constant for females of varying size ($P = .21$).

Escape Locomotion. The energetic cost of strenuous escape locomotion was greater for mating females than for solitary unladen females (fig. 4). Pooling data on solitary and mating females ($N = 66$ observations among 29 fe-

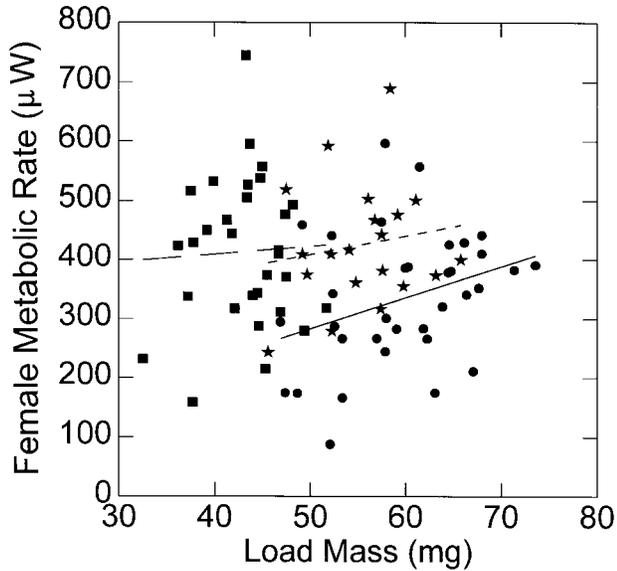


Figure 3: Relationships between female metabolic rate and the cost of transport with different types of load. Circles and solid line represent unladen females and the cost of body carriage. Squares and the coarsely dashed line represent the cost of transporting a living male in the mating position. Stars and the finely dashed line represent the cost of transporting a metal weight. Female body mass is not included in the latter two loads.

males, with ≤ 3 observations per individual), and adjusting for variation in the duration of escape locomotion using multivariate ANOVA yielded the following equation describing the energetic cost in μW (E) of each second per minute of escape locomotion (L_e) in relation to mating status ($M = 1$ if mating, 0 if solitary):

$$E = 355.8 + 131.7 \cdot M + 12.1 \cdot L_e + 11.0 \cdot L_e \cdot M. \quad (3)$$

The adjusted least-square means of the cost of escape locomotion were $400.2 \mu\text{W}$ ($\text{SEM} = 16.6$, $N = 37$) and $572.2 \mu\text{W}$ ($\text{SEM} = 20.4$, $N = 29$) for solitary and mating females, respectively. The analysis indicates that the average cost of escape locomotion is 43% higher for mating females ($F = 22.8$, $\text{df} = 1$, $P < .0001$) and that the rate at which additional escape locomotion increases MR is also greater when mating, the latter being revealed by a significant interaction between context and the duration of escape locomotion ($F = 5.32$, $\text{df} = 1$, $P = .025$).

In a multivariate analysis using pooled data on females carrying live males ($N = 29$) or solder weights ($N = 22$), we controlled for female body mass, the mass of the load, and the duration of escape locomotion. We again found a significant effect on MR of female body mass ($F = 10.04$, $P = .0027$) and the duration of escape locomotion ($F = 11.70$, $P = .001$), but no effect for the type of load (i.e., male vs. solder; $F = 0.198$, $P = .658$), indicating that mating males do nothing to ease an active female's energetic costs during escape locomotion. In fact, adjusted least-square mean costs were $442.7 \mu\text{W}$ ($\text{SEM} = 24.8$) for females carrying males and $421.4 \mu\text{W}$ ($\text{SEM} =$

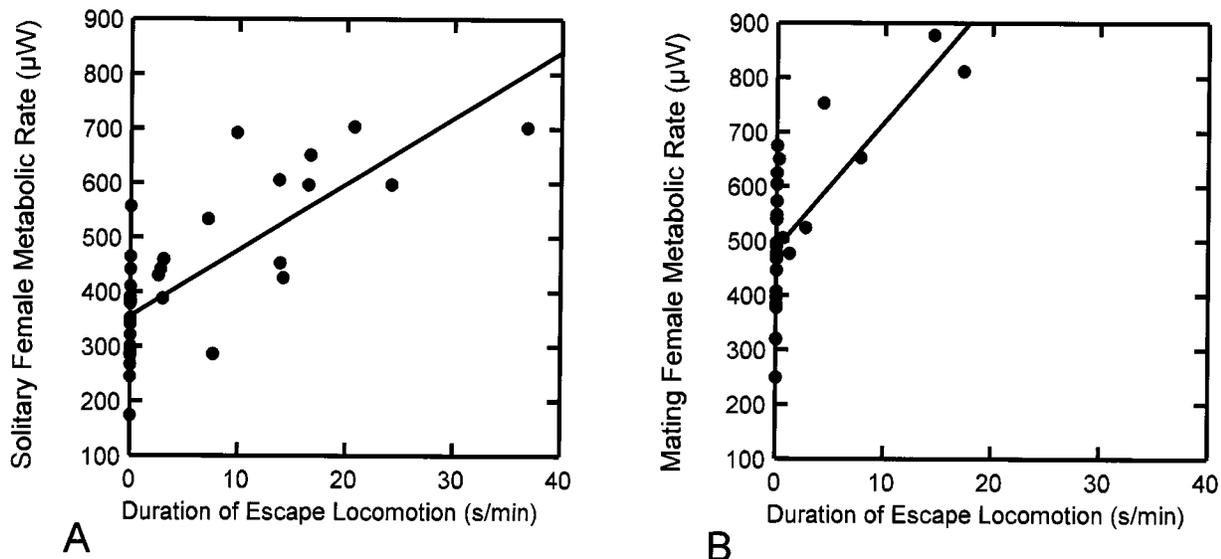


Figure 4: Relationship between the amount of time spent in escape locomotion versus the energy expenditure of (A) solitary unladen females ($r = 0.76$, $N = 37$, $P < .001$; $r^2 = 0.58$) and (B) mating females ($r = 0.68$, $N = 29$, $P < .001$; $r^2 = 0.46$). The slope of the relationship is significantly greater for mating females ($F = 5.37$, $P = .028$).

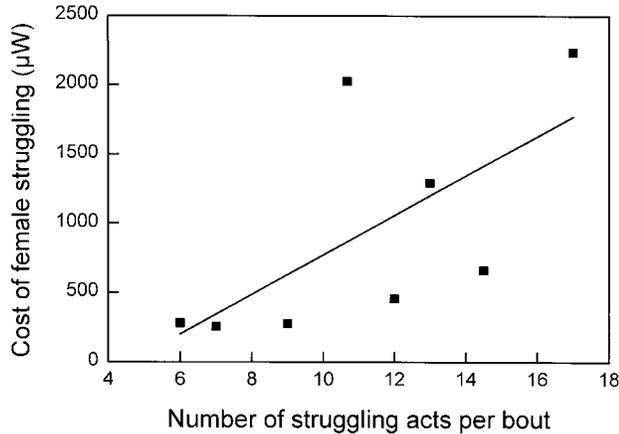


Figure 5: The energetic cost of pre-mating struggling bouts versus the number of discrete struggling acts per bout ($r = 0.726$, $N = 8$, one-tailed $P = .021$; $r^2 = 0.53$).

30.4) for females carrying solder weights. Thus, in contrast to the situation during cruising locomotion, males may be slightly more expensive for females to transport during escape locomotion than dead weight.

Energetic Cost of Struggling

Our data set on the energetics of this activity is small, but the data we obtained were clear enough for us to feel confidence in the energetic estimates. Females consumed an average of 936.6 μW during pre-mating struggling activity (SD = 813.7; $N = 8$ independent observations; three observations are average values, since the cost of struggling was measured twice in two of the eight pairs and three times in one pair). Thus struggling costs 126% more than cruising with a male in mating position, and 64% more than escape locomotion with a male. As expected, the cost of struggling was positively correlated with the number of struggling acts (i.e., leans, flips, or dunks; see appendix) recorded in each bout (fig. 5). The regression equation giving the cost of struggling in microwatts (C_s) in relation to the number of struggling acts (A) is

$$C_s = -49047 + 7512.3 \cdot A. \quad (4)$$

We found a marginally significant indication of a positive relationship between the cost of struggling and the weight of the male riding on the female ($r = 0.604$, one-tailed $P = .057$). Female mass was not significantly related to the cost of struggling ($r = -0.398$, one-tailed $P = .165$). Multiple regression using male and female body mass to predict the cost of struggling explained 48.7% of the variance. The average male mass in these

eight pairs was 42.7 mg and average female mass was 57.6 mg.

Discussion

The problem of accurately measuring the energetic costs of various behaviors is one of the empirical barriers hindering progress in behavioral ecology. Our study provides novel quantitative data on the energetic costs of male-female interactions and shows that current flow-through respirometry techniques open up new experimental possibilities in behavioral ecology (see also Watson and Lighton 1994). We were able not only to provide quantitative estimates of the basic energetic costs of locomotion in this surface dwelling insect but also to assess experimentally the energetic costs of mating. Below, we first discuss how the basic cost of locomotion compares with similar estimates in other taxa. We then discuss the various energetic costs of mating and their bearing on sexual conflicts and mating system evolution in water striders.

The Energetic Costs of Locomotion

The data presented here provide the first estimates of the energetics of pedestrian locomotion involving movement across a water surface. Our estimate of the cost of moderate locomotion in *Aquarius remigis* ($82 \text{ J kg}^{-1} \text{ m}^{-1}$, for females averaging 59.7 mg in mass) is on the low end of existing estimates of the minimum cost of voluntary pedestrian locomotion (MCOT) for tracheated limbed arthropods. To our knowledge, the lowest previously published minimum transportation cost for an arthropod of roughly similar size, $89.3 \text{ J kg}^{-1} \text{ m}^{-1}$, comes from the giant red velvet mite, *Dinothrombium magnificum*, with a mean mass of 32 mg (Lighton and Duncan 1995; the mass-scaling exponent of MCOT on body mass is about -0.3). Lighton and Duncan (1995) presented a regression line relating MCOT, in $\text{J kg}^{-1} \text{ m}^{-1}$, to body mass in g (m) in 10 ant species:

$$\text{MCOT} = 30.9 \cdot m^{-0.312}. \quad (5)$$

Using the average mass of *A. remigis* females for whom we have estimates of the cost of cruising locomotion (0.0597 g), this equation predicts an MCOT of $74.5 \text{ J kg}^{-1} \text{ m}^{-1}$. The observed MCOT of $82 \text{ J kg}^{-1} \text{ m}^{-1}$ is 110% of the predicted value, a small difference well within the range of the residuals from the original ant data (see Lighton and Duncan 1995, fig. 4). It appears that, if anything, skimming on a water surface is slightly less efficient than ant-style terrestrial locomotion.

The mass-scaling equation of Full and Tu (1991) overestimates the energetic cost of locomotion for *A. remigis*,

predicting an MCOT of $250 \text{ J kg}^{-1} \text{ m}^{-1}$. The overestimate may be due in part to the use of treadmill-based energetic measurements in the estimation of this equation. Lately, it has become apparent that estimates of locomotor costs based on treadmill experiments may yield higher estimates of energy consumption than those based on voluntary locomotion (see Lighton and Duncan 1995). The inflation factor was found to be 72% for *Pogonomyrmex rugosus* (Lighton and Feener 1989). Our measure of the cost of locomotion in *A. remigis* is thus in line with measures of voluntary locomotion in other insects.

The Energetic Costs of Mating

Wilcox (1984) showed that female *Gerris* (= *Aquarius*) *remigis* carrying guarding males did not have to actively reject single males attempting copulation, whereas single females had to struggle to reject harassing males. Mating females thus suffered less interference from single males during foraging and, as a result, enjoyed increased foraging success. However, it is clear from our study that this beneficial effect comes at a certain cost, and a cost-benefit analysis is necessary in order to elucidate whether mating is truly beneficial for females (cf. Wilcox 1984; Rowe et al. 1996).

Costs of Mate Guarding/Mate Carrying. Several previous studies have demonstrated an increased risk of predation to females while carrying males in water striders: predation risk of mating females is approximately twice that of single females (Arnqvist 1989; Fairbairn 1993; Rowe 1994). Further, females carrying males are less mobile, having shorter stride length and lower speed, than single females (Arnqvist 1989; Fairbairn 1993). The current study has shown that, in addition to these costs, mating involves significant energetic costs to females as a result of transporting passive males during copulation and mate guarding. Our estimates of this cost, both when transporting a live male and a lead weight (simulating the weight of a male), show that the female energetic expenditure during mating is at least 1.2 times that of single females locomoting at the same speed. To our knowledge, this is the first demonstration and quantification of a female energetic cost of transporting males during mating. It is worth noting that the increase in energetic expenditure is not quite proportional to the relative weight of the total load (the average weight of a mating pair is 1.7 times that of a single female) and that females are as efficient in transporting additional loads as they are additional body mass. To a certain extent, these findings confirm Fairbairn's (1993) conclusion that females appear well adapted to carrying an increased load. Other insects

that routinely transport loads also have been shown to be extraordinarily efficient (e.g., harvester ants; Weier et al. 1995).

The efficiency of male transport was high during routine cruising locomotion, its unit cost averaging less than the cost of own body carriage and carrying a soldier weight. However, during escape locomotion the unit cost of carrying a male exceeded that of the soldier weight. Although neither of these tendencies were statistically significant, the observations have heuristic value. It makes sense from the mating male point of view to keep the costs of female consensual behaviors low (e.g., moderate, steady locomotion), thereby lessening her motivation to begin resisting. In contrast, costs of female behaviors that could serve to dislodge the male (e.g., escape locomotion) should certainly not be reduced and may even be actively increased by the male to discourage females from performing them.

Costs of Male Harassment/Premating Struggles. Single female water striders facing males attempting copulation can reject these only by engaging in a pre-mating struggle, during which the females perform a series of different reluctance behaviors (see Arnqvist 1997). Struggling increases the risk of predation to females (Rowe 1994). Our study shows that struggling is also energetically costly for females; struggling females experience a dramatic increase in energetic expenditure of around 200%, compared with nonstruggling mating females engaged in cruising locomotion. Thus, since female pre-mating struggles in these insects result in female choice (indirectly; see Arnqvist 1992, 1997; Sih and Krupa 1992; Krupa and Sih 1993; Rowe 1994; Rowe et al. 1994), our results provide the first direct empirical evidence of a substantial energetic cost of female choice.

Best of a Bad Job: Convenience Polyandry. Several authors have argued that female water striders may be better off by accepting superfluous and costly copulations in the face of sexual harassment from males, since mating females avoid the costs of repelling harassing males (i.e., convenience polyandry; Wilcox 1984; Arnqvist 1989, 1992, 1997; Wilcox and Di Stefano 1991; Rowe 1992, 1994; Sih and Krupa 1992; Fairbairn 1993; Krupa and Sih 1993; Rowe et al. 1994; Weigensberg and Fairbairn 1994, 1996; Vepsäläinen and Savolainen (1995). As we have demonstrated here, however, mating females suffer a cost of transporting males during mating, and which option will be least disadvantageous (i.e., bearing the costs of rejecting harassing males versus accepting superfluous costly copulations) will depend primarily on the frequency with which males are attempting copulation (i.e., harassment rate). The results of our study for the

first time provide the basis for a quantitative test of the convenience polyandry hypothesis. Below, we provide a simple quantitative model comparing the economics of foraging for single females (rejecting all harassing males) and mating females (carrying a mating male) in *A. remigis*. This linear model assumes that females behave so as to minimize the ratio between the energetic expenditure and yield and is based solely on the energetics of matings.

Assuming that mating females suffer no, or only negligible, costs of male harassment (see Wilcox 1984; Wilcox and Di Stefano 1991; and Vepsäläinen and Savolainen 1995 for support of this assumption), that energetic fitness can be approximated by the amount of energy expended per unit of efficient foraging time gained (i.e., time undisturbed by harassing males), and that the relationship between the efficient foraging time gained and actual foraging success is identical for single (s) and mating (m) females, we can express the energetic fitness E during the time period t as

$$E_s = \mu W_1 \cdot [t - (h \cdot t')] + (\mu W_2 \cdot h \cdot t') / [t - (h \cdot t')], \quad (6)$$

for single females (spending time and energy on rejecting males by struggling), and

$$E_m = \mu W_3 \cdot t / t = \mu W_3, \quad (7)$$

for mating females (carrying a mating male), where μW_1 is the energy consumption of a single female during foraging; μW_2 is the energy consumption of a female during pre-mating struggles; μW_3 is the energy consumption of a mating female during foraging; h is the rate of male mating attempts (harassment rate); and t' is the average duration of a pre-mating struggle. These expressions, then, can be used to compare directly the performance of single and mating females. In figure 6, we have parameterized the ratio between energetic expenditure and yield as a function of male harassment rate, using the quantitative estimates of female energetic power during various behaviors (μW_i above) from the current study and an average struggle duration (t') of 16 s (see Wilcox 1984; Weigensberg and Fairbairn 1994, 1996).

Several important insights can be gained from this simple model, which is based purely on the quantitative energetic costs and benefits of male-female interactions. First, mating females are not always more successful in minimizing the ratio between energetic expenditure and yield (cf. Wilcox 1984) compared with females that resist mating. When the rate of male harassment is relatively low, single females (S_1 in fig. 6) actually expend less energy per unit of foraging time than do mating females (M in fig. 6). In this situation, convenience polyandry is not predicted despite the fact that single females have to spend time and energy on rejecting males. Second, at a

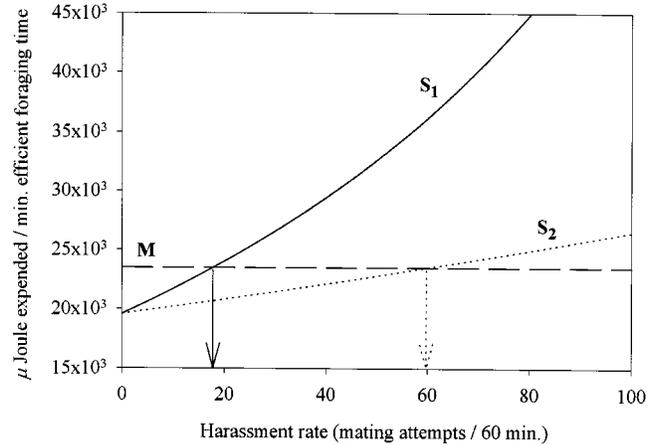


Figure 6: Energetic expenditure per minute of undisturbed foraging time for mating (M) and single (S) females at different rates of male harassment. Single females spend less energy per minute at low rates of male harassment, while mating females do better at high harassment rates. Females, on average, are expected to switch from resisting to accepting superfluous matings at the harassment rate that renders accepting superfluous matings the least costly option (indicated by arrows). This “critical” rate is determined, in part, by the amount of energy required to reject a male suitor. A reduction, for example, in the average time required to reject a male from 16 s (S_1 , solid line) to 5 s (S_2 , dotted line) leads to a corresponding shift in the switch point from approximately 20 to 60 mating attempts per hour.

certain harassment rate threshold, accepting superfluous matings becomes the “best of a bad job” for females (cf. Arnqvist 1989; Rowe 1992) and convenience polyandry is expected. Our results indicate that foraging females, on average, should cease rejecting harassing males at a “critical” harassment rate of approximately 20 mating attempts per hour in *A. remigis* (see fig. 6), a quantitative prediction that could be tested empirically in this species. However, additional factors (e.g., predation risk, food availability, satiation level, water current, different relationships between foraging time and success for single and mating females) could affect the total female cost-benefit balance in complex ways. While these are very unlikely to affect our main conclusions, they may alter the predicted harassment rate threshold quantitatively. Third, even if variance within and between females in perceived harassment rate will generate variation in female mating propensity under any given average harassment rate, the convenience polyandry hypothesis predicts a nonlinear relationship between harassment rate and female mating activity, which again could be tested empirically. The relationship should basically be sigmoidal, with a relatively rapid increase in mating frequency over the harassment rate threshold domain.

In an evolutionary sense, each sex is part of the envi-

ronment of the other sex and since the evolutionary interests of the sexes often do not coincide, sexual conflicts arise. Several authors have suggested that many traits that affect the relative control of reproduction evolve via a co-evolutionary arms race between the sexes (Arnqvist and Rowe 1995; Rice 1996; Alexander et al. 1997). The dynamics of mating systems in water striders should to a large extent depend on the evolved current relative abilities of the sexes to control reproduction (Arnqvist 1997). If females evolved morphological or behavioral traits that increased their efficiency at rejecting males, by decreasing the time or the energetic power required to do so, this would alter the predicted mating system. Our model above can exemplify this phenomenon. The average time required to reject a harassing male in *A. remigis* is approximately 16 s (Wilcox 1984; Weigensberg and Fairbairn 1994, 1996), although this is likely to vary according to male insistence, which varies in turn with factors such as male population density (Lauer et al. 1996). A situation where rejection time was reduced to 5 s would lead to an approximate shift in the harassment rate threshold domain from 20 to 60 mating attempts per hour (cf. S_1 vs. S_2 in fig. 6), leading not only to a higher absolute energetic fitness for females in the population but also to alterations in many mating system parameters (e.g., overall mating activity).

Costs of Loading and Selection on Male Body Size. Fairbairn (1990, 1993) suggested that costs of mate carrying may select for males that are small relative to their mates and, thus, affect the evolution of sexual size dimorphism. In contrast to this suggestion, however, several field studies have shown that male size is generally positively correlated to reproductive success (Sih and Krupa 1992; Arnqvist et al. 1996; Rowe and Arnqvist 1996; Arnqvist 1997). The size of the male may affect both the energetic costs of mate carrying and those of rejecting harassing males. Although cruising while carrying a male clearly costs females more than cruising without a male, our data provide no evidence of natural selection acting to reduce male size to ameliorate the costs of carrying to females. Within the range of male weights we utilized, there was no significant relationship between estimated female power consumption and male mass, with or without adjustment for female mass. In contrast, the limited amount of data available on struggle costs indicated that female energy consumption during the premating struggle was indeed positively related to male mass.

The results of the current study thus suggest that while the energetic cost of carrying males during mating per se is at most only very weakly related to male size, the cost of rejecting males is more strongly related to male size. One prediction from this observation is that *A. remigis* females should engage in premating struggles for a

shorter time with large males than with small males, since struggles with large males are more energetically costly per unit of time. Interestingly enough, such a pattern was observed in *A. remigis* by Weigensberg and Fairbairn (1996). This mechanism would also lead to a higher acceptance rate of large males, provided that females reject all male mating attempts with equal total "effort." Again, this prediction is upheld by observations: large male mating advantage is a very commonly found nonrandom mating pattern in natural water strider populations (Sih and Krupa 1992; Arnqvist et al. 1996; Rowe and Arnqvist 1996). In conclusion, considerations of energetic costs of mating generates predictions of nonrandom mating by size in water striders that are well supported by empirical observations. In contrast to the suggestions by Fairbairn (1990, 1993), however, the energetic costs of loading during mating is predicted to generate selection for large males.

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APPENDIX

Operational Definitions of Behaviors

Stationary. The strider(s) floats motionless on a nonmoving water surface; provides an estimate of the resting metabolic rate.

Cruising Locomotion. The strider(s) treads a water surface set in circular motion at standard speed (ca. 4.19 m min^{-1}), such that the strider maintains its position on the water surface.

Escape Locomotion. This behavior is characterized by highly erratic or sustained unidirectional locomotion on a water surface set in standard circular motion (as for cruising locomotion), such that the strider rapidly and repeatedly leaps forward into the glass wall of the flask. Striders in nature typically use this kind of rapid, frenetic, sprinting locomotion to escape predators, harassing conspecifics, or an otherwise acutely unfavorable micro-environment.

Struggling. This constitutes various female behaviors whereby the female attempts to dislodge a male mounted in the normal mating position. Struggling includes “leans” (flexing one or more legs thus tilting her body out of the normal horizontal position resulting in the water surface pushing up against the male’s legs or body), “flips” (leaping up to land on her side or back), and “dunks” (diving forward and down to partially submerge part of her body and the male’s).

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