Developmental costs of male sexual traits in the water strider *Rheumatobates rileyi*

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Abstract: Natural selection is thought to impose costs on sexually selected traits and thereby constrain their evolutionary modification. Where sexually selected traits involve increases in size or structural elaboration, development of the traits may be costly. Males of some species in the water strider genus *Rheumatobates* have dramatically elaborated antennae and legs. In a pair of experiments on *Rheumatobates rileyi*, we tested the hypothesis that in males, the development rate is decreased and mortality increased relative to unelaborated females during the final instar, when these traits were substantially developed. In the first experiment, we reared individual larvae through to adult that were brought into the laboratory during the third, fourth, and fifth (final) instars. The development rate was reduced and the mortality increased during the final intermolt period in males relative to females. The effect on development rate was highly significant, but the effect on mortality was not. Notably, there was no effect of sex on the duration of the fourth instar, when male modifications are not expressed. In a second experiment, 4 potentially cannibalistic adults were included with fifth-instar larvae. We found no effect of potential cannibals on either development rate or mortality of instars. However, as in the first experiment, the development rate was significantly reduced in males relative to females. Mortality of males was also higher than that of females, although this effect was not significant. Meta-analysis of all our mortality results indicate that mortality of developing fifth-instars was higher in males than in females. Our results are consistent with the hypothesis that development of elaborate sexual traits in male *R. rileyi* is costly.

Résumé : La sélection naturelle est réputée imposer des coûts à l'évolution de certains caractères sexuels et en limite donc les modifications évolutives. Dans les cas où ces caractères sexuels supposent des augmentations de taille ou des modifications structurales, l'expression de ces caractères peut être coûteuse. Les mâles de certaines espèces de patineurs du genre *Rheumatobates* ont des antennes et des pattes remarquablement élaborées. Au cours d'une paire d'expériences sur *Rheumatobates rileyi*, nous avons éprouvé l'hypothèse selon laquelle la vitesse de développement est retardée et le taux de mortalité augmente chez les mâles par comparaison à des femelles à antennes et pattes non élaborées au dernier stade, moment où ces caractères sont déjà bien développés. Au cours de la première expérience, nous avons élevé des larves jusqu'au stade adulte, larves qui ont été apportées au laboratoire au cours des stades 3, 4, et 5 (stade terminal). Au cours de la dernière intermue, la vitesse de développement est devenue plus faible et la mortalité plus élevée chez les mâles que chez les femelles. La diminution de la vitesse de développement était significative, l'augmentation de la mortalité ne l'était pas. Le sexe n'avait pas d'effet sur la durée du quatrième stade, puisque les modifications structurales des mâles n'étaient pas encore exprimées. Dans une deuxième expérience, quatre adultes présumés cannibales ont été mis en présence de larves de cinquième stade. Ni la vitesse de développement ni le taux de mortalité des larves n'ont été affectés. Cependant, comme dans la première expérience, la vitesse de développement des mâles était significativement ralentie par rapport à celle des femelles. Le taux de mortalité des mâles était également plus élevé que celui des femelles, mais cet effet n'était pas significatif. Une méta-analyse de tous nos résultats sur la mortalité indique que la mortalité des larves mâles en développement au cinquième stade est plus élevée que celle des femelles. Nos résultats corroborent l'hypothèse selon laquelle le développement de caractères sexuels élaborés chez *R. rileyi* est coûteux.

[Traduit par la Rédaction]

Introduction

Models of evolution by sexual selection predict that traits subject to female preference will evolve in the preferred direction until costs imposed by expressing these traits balance the benefits gained under sexual selection. Thus, natural selection is thought to constrain the action of sexual selection on male traits (reviewed in Bradbury and Andersson 1987; Kirkpatrick and Ryan 1991; Andersson 1994). Potential costs of exaggerated secondary sexual characteristics include increased predation risk, reduced foraging success, and decreased development rate. It is therefore necessary to identify and determine these costs in order to understand the joint effect of sexual and natural selection on sexually selected traits (Partridge and Endler 1987; Kirkpatrick and Ryan 1991; Schluter et al. 1991; Andersson 1994). Costs may be divided into three overlapping classes, those associ-

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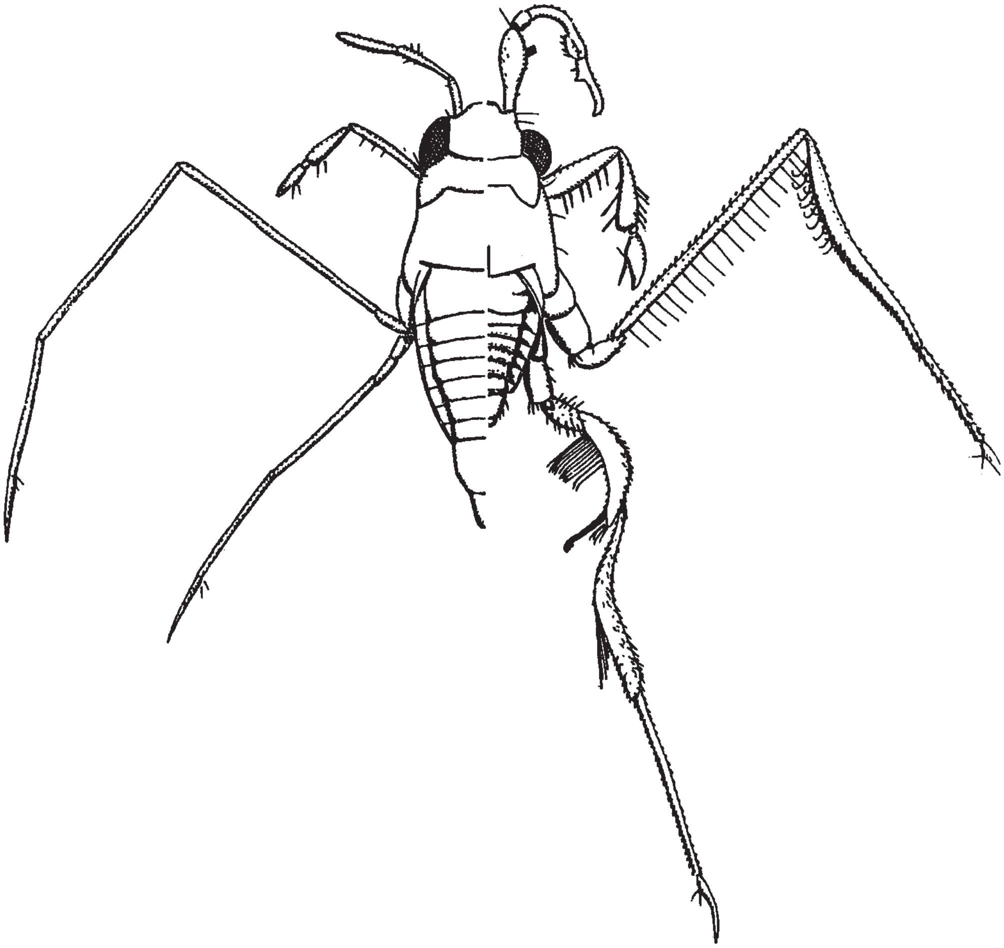
Fig. 1. Partial line drawing of adult male (right) and female (left) *R. rileyi*, indicating the dimorphism in size and modification of the antennae and legs.



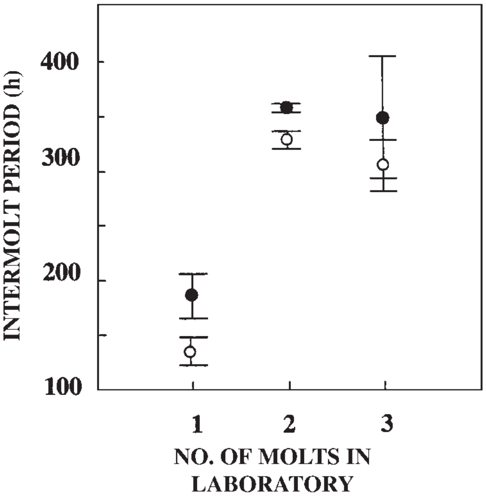
ated with use of the trait (e.g., displays and calls), with possessing the trait (e.g., the aerodynamic costs of elongated tails), and with building the trait during development.

The last class has received little attention, despite the view that developmental costs may be common (Partridge and Endler 1987). Sexual selection for large body size in males is one case where developmental costs are likely. In *Drosophila melanogaster*, for example, large males have higher mating success (Partridge and Farquhar 1983; Partridge et al. 1987), but artificial selection for large body size in this species results in a longer larval period (Robertson 1960), and an increase in larval mortality under some conditions (Partridge and Fowler 1992). In molting organisms, the evolution of complex secondary sexual traits may be constrained by their costly interference with the molting process. In the chernetid pseudoscorpion *Dinocheirus arizonensis*, males possess enlarged pedipalps, which are used to initiate mating by forcefully grasping females (Zeh 1987*a*, 1987*b*). However, the increase in pedipalp size is associated with prolonged nymphal development (Zeh 1987*b*). Similarly, sexually selected elaborations of the integument in males of the water strider *Gerris odontogaster* (Arnqvist 1994) and the mayfly *Dolania* sp. (Peters and Peters 1986) appear to interfere with the molting process and thereby increase mortality at molt. In *G. odontogaster*, the duration of the ultimate molt is extended in males, resulting in increased exposure to cannibalism, and in *Dolania* sp., elaborated male legs become stuck in the partially shed exuviae.

One of the most striking cases of sexual dimorphism occurs in the water strider genus *Rheumatobates* (Fig. 1), where extreme modifications of the antennae, fore, mid, and hind legs, abdomen, and genitalia occur in males. As is typical of water striders (Rowe et al. 1994; Arnqvist 1997), the mating behavior of *R. rileyi* Bergroth, 1892 (one of the more highly elaborated species in the genus) is characterized by intense sexual conflict over the mating decision (Westlake 1998). Males use their elaborated antennae and hind legs to forcefully grasp females during premating struggles and therefore increase control over the outcome. Therefore, we expect strong sexual selection on these modifications. *Rheumatobates rileyi* passes through five instars prior to the final adult molt and it is in this final molt that the dimorphic characters are substantially expressed (personal observation; see also Silvey 1931). Slight differences between the sexes in structure of antennae and hind legs are observed first in the third to fifth instars, including thickening and elongation of these appendages in males, but it is not until the ultimate molt that the sexual dimorphism becomes dramatic.

In this study we test the hypothesis that these secondary sexual traits impose developmental costs on male *R. rileyi*. We predicted that development of these modifications would decrease the development rate and increase mortality during

Fig. 2. Relationship between the observed final intermolt period (mean ± SE) and sex for those larvae that molted once, twice, or three times during the experiment. Solid circles indicate males and open circles indicate females. Larvae in the class that molted once were collected during their final intermolt period, and this is why the observed intermolt period is so short relative to those in the other two classes (see Methods and Results for further discussion).



molt in males relative to females. Moreover, we expected these effects to occur only in the ultimate instar and molt, when these traits are substantially developed. We conducted two experiments on field-collected larval *R. rileyi* to test these predictions. In the first experiment larvae were reared individually through the penultimate and ultimate larval instars. In the second experiment we included potentially cannibalistic adults to test the additional hypothesis that mortality of males during the final molt would be elevated because of prolonged exposure to cannibals, as has been previously shown in another species (Arnqvist 1994).

Methods

Experiment 1

Larval water striders were collected in early July 1997 from natural populations inhabiting canals in Holland Marsh, just northwest of Toronto, Ontario. These larvae were maintained collectively in bins in the laboratory until the experiment. For the experiment, 220 third- to fifth-instar larvae were placed individually in water-filled pails (4.5L), fed every other day with 4 frozen fruit flies per individual, and kept at an ambient temperature of 22°C (±2°C). Molting fate (dead or alive) and duration of the observed intermolt period were recorded for each individual. We used intermolt period as an index of development rate. Larvae were reared to the adult stage or until they died. During the experiment, 28 larvae died for unknown reasons (not at molt) or escaped. We did not consider these any further because we were interested only in those that died during molt. Of the remaining 192 larvae, 109 began the experiment as fifth-instar larvae (45 males, 64 females), 76 as fourth-instar larvae (35 males, 41 females), and only 7 as third-instar larvae (5 males, 2 females).

Experiment 2

In late July 1997, 120 fifth-instar larvae were collected and maintained as above. There were 4 potential cannibal × sex experimental treatments (2 × 2). In treatments 1 and 2, larvae of each sex were held individually as in experiment 1, and in treatments 3 and 4, larvae of each sex were held individually with 4 adults (2 males and 2 females) that served as potential cannibals. There were 30 replicates per treatment. Experimental individuals were placed in water-filled pails (4.5 L) and kept at an ambient temperature of 22°C (±2°C). Experimental individuals (both larvae and cannibals) in all treatments were held at low food availability and then starved periodically to enhance the potential for cannibalism. All treatments were subjected to the same feeding schedule. In detail, the food limitation/starvation schedule was as follows: each individual was fed 1 fly for the first 34.6 h, starved for the next 67.5 h, fed 2 flies over the next 52.0 h, starved for the next 20.0 h, and fed 1 fly for the remaining 56.8 h of the experiment. Individuals were fed again after only 20.0 h of starvation near the end of the experiment because mortality was high, presumably resulting in part from starvation. Larvae were reared to the adult stage or until they died. Molting fate (dead or alive) and intermolt period was recorded for each individual. Dead cannibals were replaced in the experiment as necessary.

Table 1. Results of ANOVA on the effect of sex on the final intermolt period for individuals in which this molt is their first or second molt completed in the laboratory.

Source	df	Mean square	*F* ratio	*p*
First molt				
Sex	1	63493.029	4.903	0.029
Error	102	12949.473		
Second molt				
Sex	1	16169.422	9.495	0.003
Error	71	1702.855		

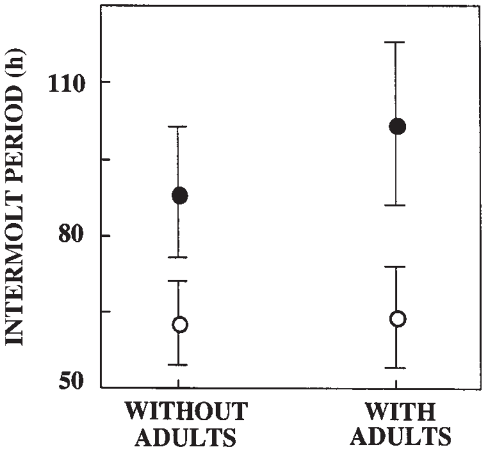
For the analysis of development rates in both experiments, data for individuals that died while molting or that emerged deformed were excluded. Intervals between check times varied significantly throughout the experiment, owing to practical considerations, therefore the midpoint between the last check time and the time that individual had molted was used as an estimate of molt time.

Results

Development rate

The final intermolt period was significantly longer in males than in females in the first experiment (Fig. 2, Table 1). For individuals in which this molt was their first, second, or third molt in the laboratory, the observed male intermolt period was, on average, 37.4% (50.6 h), 9.1% (30.0 h), or 14.1% (43.3 h) longer, respectively, than that of females. We note that some development of fifth instars had occurred prior to their collection for the experiment. This is why their intermolt period is so low (see the points at the left of Fig. 2). Therefore, it is possible that females had a shorter intermolt period in part because of some accumulated effects prior to the experiment. For example, females may hatch more quickly than males, and if there were synchrony of egg laying within a sex, then females would be further into the fifth instar when collected. Alternatively, development may simply have been faster for females than males in the field. To control for either possibility, we analyzed results separately for larvae that had undergone the molt to the fifth instar in the laboratory and those that were collected in fifth instar. It appears that the latter group of individuals entered the experiment about midway into the fifth instar (Fig. 2). Nevertheless, these analyses demonstrate that

Fig. 3. Relationship between the observed final intermolt period (mean ± SE) and sex for larvae reared in the presence and absence of adults. Solid circles indicate males and open circles indicate females.



males of both groups had significantly longer intermolt periods (Table 1). Thus, any effects from the field do not appear to have biased our results. Given the small sample size (6) of individuals in which this molt was their third molt in the laboratory, analysis was not appropriate but the pattern was consistent.

As predicted, there was no sexual difference in the development rates of fourth instars (ANOVA, $F_{[1,74]} = 0.023$, $p = 0.881$). Observed intermolt periods for males and females were 72.6 h ($n = 35$, SE = 9.94 h) and 74.5 h ($n = 41$, SE = 8.19 h), respectively. Note that all of these individuals entered the experiment part way through their fourth instar.

In the second experiment, the final intermolt period was similarly significantly longer in males than in females (Fig. 3, Table 2).With and without potentially cannibalistic adults, males took 59.2% (38.0 h) and 41.0% (26.0 h) longer than females. The intermolt period was not significantly affected by the presence of adults or the interaction between adults and sex (Table 2).

Molting mortality

As predicted, molting mortality was greater in males than in females in the final molt in both experiments. In the first experiment, the data were analyzed separately by the number of molts completed in the laboratory (Table 3). Males suffered higher mortality than females during the final molt in each case, but not significantly so. For those individuals in which this molt was their first in the laboratory, males suffered 8.9% mortality, while females suffered 1.6% ($\chi^2 = 1.783$, $p > 0.1$), and for those in which this molt was their second in the laboratory, males suffered 5.9% mortality, while females suffered none ($\chi^2 = 0.730$, $p > 0.25$). A test of significance was not appropriate for individuals in which this molt was their third in the laboratory, given the small sample size (6); there was no mortality in either sex in this group. There was no mortality during the fourth- to fifth-instar molt.

In the second experiment, the analysis of a sexual difference in mortality during the final intermolt period was complicated by the apparent effect of starvation on survival. A significant jump in mortality was observed at 164.5 h (5 males and 2 females died). The problem lies in the fact that all females, except the 2 that died, had completed molting by the time this second starvation period was experienced at 155–174 h. In contrast, many males from both treatments 1 and 3 had not yet molted; they experienced this second starvation period as larvae and likely suffered an increase in mortality as a result. In order to be conservative and remove this potential bias toward male mortality, data collected after this second starvation period were excluded from the analysis.

Table 2. Results of ANOVA on the effect of sex and presence of potentially cannibalistic adults on final intermolt period.

Source	df	Mean square	*F* ratio	*p*
Sex	1	23222.759	7.315	0.008
Adults	1	1232.484	0.388	0.535
Sex × adults	1	846.572	0.267	0.607
Error	88	3174.512		

Although males suffered higher mortality in the presence and absence of adults, the difference in mortality between the sexes was not significant in either case (Table 4). Without adults, males suffered 20.7% mortality and females 11.1% ($\chi^2 = 0.373$, $p > 0.5$), and with adults, males suffered 16.7% mortality and females 7.4% ($\chi^2 = 0.347$, $p > 0.5$). Surprisingly, we found no effect of these potentially cannibalistic adults on mortality (the two samples were homogeneous; heterogeneity $\chi^2 = 0.603$, $p > 0.25$)

Although male mortality was greater than female mortality in all four tests performed, none of the tests yielded statistically significant results. This may be due in part to the relatively small sample size in each test. To increase our power, we conducted a meta-analysis of these four independent tests (first and second molts completed in the laboratory in the first experiment and with and without adults in the second experiment). We used the methods outlined by Kirby (1993) and Cooper and Hedges (1994). In brief, we first transformed our χ^2 statistics to Pearson product-moment coefficients, *r*, and then to Fisher's Z_r. These are our measures of effect size. Effect sizes were then weighted by the sample size of each analysis. The weighted mean effect size was 0.104 and this was just significantly different from zero ($p < 0.05$, one-tailed test). We used a one-tailed test because our a priori hypothesis was directional.

Of the 22 deaths observed during final molt in these experiments, 18 (14 males and 4 females) died during the process of molting. The remaining 4 individuals completed the molt but died immediately thereafter (1 female) or were so deformed (2 males, 1 female), we concluded that they would not have survived in nature.

Discussion

Our study demonstrates that male *R. rileyi* take longer to pass through the final instar and suffer greater mortality during the final molt than do females. These results are consistent with the hypothesis that development of the remarkable elaboration of male secondary sexual characteristics in this species have come at a cost. Such costs are predicted by most models of trait evolution under sexual selection when

Table 3. Mortality of the sexes during the final molt according to the number of molts completed in the laboratory.

	First molt		Second molt		Third molt	
	Males	Females	Males	Females	Males	Females
No. dead	4	1	2	0	0	0
No. alive	41	63	32	41	4	2
Mortality (%)	8.9	1.6	5.9	0	0	0

Table 4. Mortality of the sexes during the final molt in the presence and absence of potentially cannibalistic adults.

	Without adults		With adults	
	Males	Females	Males	Females
No. dead	6	3	4	2
No. alive	23	24	20	25
Mortality (%)	20.7	11.1	16.7	7.4

the trait is at or approaching equilibrium (Bradbury and Andersson 1987; Kirkpatrick and Ryan 1991; Andersson 1994). Although developmental costs of sexually selected traits are expected to be common, supporting evidence is sparse (see Introduction). Below, we discuss the evidence for developmental costs of male modifications in *R. rileyi*.

In both experiments, male development was increased by about 26–50 h compared with that of females. Based on a total final-instar duration for females of approximately 300 h in laboratory rearings (Fig. 2), this represents a 9–17% increase. Notably, this intersexual difference occurred only in the final instar. Intermolt period from the fourth to the fifth instar was equivalent between the sexes. This was expected because it is only during the final instar that morphology diverges greatly (Silvey 1931). Presumably, the male development rate is decreased because of the time required to construct the elaborate modifications.

We are aware of three other cases where a similar time cost to development of secondary sexual characters has been suggested. Male *D. arizonensis* have enlarged pedipalps that are used for forcefully grasping the female during initiation of mating (Zeh 1987*a*, 1987*b*). Zeh (1987*b*) reported that total larval development time was greater in males than females. However, there was no attempt to associate the period of divergence in morphology with the period of divergence of development times, as we have done here. Hunt and Simmons (1997) report that the expression of horns (a secondary sexual trait) retards development in males of the horned beetle *Onthophagus taurus*. Finally, in *G. odontogaster*, adult males, but not larvae, possess abdominal processes used to grasp the female during premating stuggles (Arnqvist 1989). Arnqvist (1994) has demonstrated that final molt duration is greater in male (*G. odontogaster*) than in females. He argues that this may result from the physical challenges of removing these processes from the exuviae during molt. It would be intriguing to measure molting duration in *R. rileyi*, where we may similarly expect male traits to impede the process.

Our results on molting mortality similarly support the hypothesis that there are developmental costs to male modifications in *R rileyi*. We found increased mortality of males (during the final molt) in both experiments. Although individual tests of these differences did not attain significance, subsequent meta-analysis of the entire data set revealed a significant increase in male mortality. Elevated male mortality in our experiments resulted from incomplete and unsuccessful molts. Mortality typically occurred during the mid and latter stages of the molt as larvae were attempting to extract themselves from the exuvium. We propose that this resulted from the mechanical difficulties of extracting the extreme modifications of their secondary sexual characters.

An example that parallels this type of developmental constraint in *R. rileyi* occurs in *G. odontogaster.* The length of the sexually selected abdominal processes in males is positively related to the duration of the ultimate larval molt, presumably because the processes constitute a mechanical hindrance during molting (Arnqvist 1994). This notion was supported by laboratory observations of fifth-instar larvae actually getting stuck in the abdominal region of the exuvium during the ultimate molt (G. Arnqvist, unpublished data). Another example of this kind of developmental constraint is found in mayflies of the genus *Dolania* (Peters and Peters 1986). The legs of these mayflies are sexually dimorphic and frequently break off during the ultimate molt in males and get stuck in the subimaginal exuvium.

Unexpectedly, the presence of potentially cannibalistic adults did not increase mortality for either sex in the second experiment. In other water strider species, rates of cannibalism are relatively high and molting larvae are particularly vulnerable (e.g., Andersen 1982; Arnqvist 1994). Cannibalism of molting individuals (almost always males) has been observed in laboratory communal pools at higher densities in *R. rileyi*, but it is not clear how prevalent this is. Repeating the experiment using known natural predators would be instructive.

There is anecdotal evidence of a cost of male secondary sexual modifications under more natural conditions in another highly elaborated species of *Rheumatobates*, *R. aestuarius*. In a series of field collections the adult sex ratio was 1:2, yet among the fifth-instar larvae, the sexes were more or less equally represented (1.2:1) (Cheng and Lewin 1971). Cheng and Lewin (1971) suggest the possibility that males exhibit greater adult mortality or shorter longevity than females, but it is also possible that males suffer higher mortality during the final molt, as do those of *R. rileyi*. In *R. aestuarius*, as in *R. rileyi*, male secondary sexual modifications are not significantly expressed until the final molt (Cheng and Lewin 1971).

In summary, our data are consistent with the hypothesis that the increase in development time and molting mortality of males represent developmental costs of secondary sexual traits. Yet, as in previous examples, they remain only correlative. For example, differences in instar duration occur in a variety of other species of water striders in the genus *Limnoporus* (e.g., Klingenberg and Spence 1993), where dramatic dimorphisms are not present. Differences are not consistent between species, occur at various instars during development, may appear, disppear, or even change sign during development, and are rarely significant (Klingenberg and Spence 1993). Thus, the evolutionary or functional correlates of these developmental differences are not known. The genus *Rheumatobates* may provide an ideal group to isolate correlates of differences in development. The presence and degree of modification of male secondary sexual characteristics vary dramatically within the genus, and a phylogeny has been proposed (Westlake 1999). A comparative test of the evolutionary correlation between male modification and differences in development time and molting mortality between the sexes would be most informative.

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References

Andersen, N.M. 82. The semiaquatic bugs (Heteroptera, Gerromorpha): phylogeny, adaptations, biogeography and classification. Entomonograph Vol. 3. Scandinavian Science Press Ltd., Klampenborg, Denmark.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, N.J.

Arnqvist, G. 1989. Sexual selection in a water strider: the function, nature of selection and heritability of a male grasping apparatus. Oikos, **56**: 344–350.

Arnqvist, G. 1994. The cost of male secondary sexual traits: developmental constraints during ontogeny in a sexually dimorphic water strider. Am. Nat. **144**: 119–132.

Arnqvist, G. 1997. The evolution of water strider mating systems: causes and consequences of sexual conflicts. *In* The evolution of mating systems in insects and arachnids. *Edited by* J.C. Choe and B.J. Crespi. Cambridge University Press, Cambridge. pp. 146–163.

Bergroth, E. 1892. Note on the water-bug, found by Rev. L. Zabriskie. Insect Life, **4**: 321.

Bradbury, J.W., and Andersson, M.B. 1987. Sexual selection: testing the alternatives. John Wiley and Sons, Chichester.

Cheng, L., and Lewin, R.A. 1971. An interesting marine insect, *Rheumatobates aestuarius* (Heteroptera: Gerridae), from Baja California, Mexico. Pac. Insects, **13**: 333–341.

Cooper, H., and Hedges, L.V. 1994. The handbook of research synthesis. Russell Sage Foundation, New York.

Hunt, J., and Simmons, L.W. 1997. Patterns of fluctuating asymmetry in beetle horns: an experimental examination of the honest signalling hypothesis. Behav. Ecol. Sociobiol. **41**: 109–114.

Kirby, K.N. 1993. Advanced data analysis with Systat. Van Nostrand Reinhold, New York.

Kirkpatrick, M., and Ryan, M.J. 1991. The evolution of mating preferences and the paradox of the lek. Nature (Lond.), **350**: 33–38.

Klingenberg, C.P., and Spence, J.R. 1993. Heterochrony and allometry: lessons from the water strider genus *Limnoporus*. Evolution, **47**: 1834–1853

Partridge, L., and Endler, J.A. 1987. Life history constraints on sexual selection. *In* Sexual selection: testing the alternatives. *Edited by* J.W. Bradbury and M.B. Andersson. John Wiley and Sons, Chichester. pp. 265–277.

Partridge, L., and Farquhar, M. 1983. Lifetime mating success of male fruitflies is related to their size. Anim. Behav. **31**: 871–877.

Partridge, L., and Fowler, K. 1992. Direct and correlated responses to selection on age at reproduction in *Drosophila melanogaster*. Evolution, **46**: 76–91.

Partridge, L., Hoffman, A., and Jones, J.S. 1987. Male size and mating success in *Drosophila melanogaster* and *D. pseudoobscura* under field conditions. Anim. Behav. **35**: 468–476.

Peters, J.G., and Peters, W.L. 1986. Leg abscission and adult *Dolania* (Ephemeroptera: Behningiidae). Fla. Entomol. **69**: 245–250.

Robertson, F.W. 1960. The ecological genetics of growth in *Drosophila*. 1. Body size and development time on different diets. Genet. Res. Camb. **1**: 288–304.

Rowe, L., Arnqvist, G., Sih, A., and Krupa, J. 1994. Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. Trends Ecol. Evol. **9**: 289–293.

Schluter, D., Price, T.D., and Rowe. L. 1991. Conflicting selection pressures and life-history trade-offs. Proc. R. Soc. Lond. B Biol. Sci. **246**: 11–17.

Silvey, J.K. 1931. Observations on the life-history of *Rheumatobates rileyi*. (Berg.) (Hemiptera–Gerridae). Pap. Mich. Acad. Sci. **13**: 433–446.

Westlake, K.P. 1998. Sexual conflict and the evolution of male modification in the water strider genus *Rheumatobates* (Heteroptera: Gerridae). M.Sc. thesis, University of Toronto, Toronto, Ont.

Westlake, K.P., Rowe, L., and Currie, D.C. 1999. Phylogeny of the water strider *Rheumatobates*. Syst. Entomol. In press.

Zeh, D.W. 1987*a*. Aggression, density, and sexual dimorphism in chernetid pseudoscorpions (Arachnida: Pseudoscorpionida). Evolution, **41**: 1072–1087.

Zeh, D.W. 1987*b*. Life history consequences of sexual dimorphism in a chernetid pseudoscorpion. Ecology, **68**: 1495–1501.