

THE ENERGETIC COST OF COPULATION IN A POLYGYNANDROUS MILLIPEDE

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Summary

We determined the energetic cost of copulation in both sexes of *Alloporus uncinatus*, a polygynandrous millipede in which copulation can last for several hours and involves physical restraint of the female by the male. We found an elevation in the rate of oxygen consumption by males and a depression in the rate of oxygen consumption by females during copulation. The rate of oxygen consumption of females, but not of males, was elevated immediately after copulation, indicating that females had built up and were repaying an oxygen debt. On this basis, we estimated energy expenditure during copulation to be 30 % above

resting levels in males and 14 % above resting levels in females. As matings are frequent in this species in the wild throughout the 4 month breeding season, we suggest that the energetic demands of copulation are a previously overlooked potentially significant cost of reproduction in this species and in other invertebrate species with similar mating patterns.

Key words: millipede, *Alloporus uncinatus*, energetics, copulation, cost of reproduction, mating pattern.

Introduction

Many of the costs associated with reproduction are well documented (see, for instance, Trivers, 1972; Bell, 1980; Thornhill and Alcock, 1983; Partridge and Harvey, 1985, 1988; Reznick, 1985; Partridge, 1989; Clutton-Brock, 1991). These include costs related to territorial defence, courting, gamete development, provision of nuptial gifts (including spermatophores), mate defence and investment in the development and survival of offspring. However, there are also costs associated with the act of copulation itself, costs that can in their own right lead to reduced longevity and fitness (Bell and Koufopanou, 1985; Fowler and Partridge, 1989). For example, a suite of experiments on mating costs in fruitflies (*Drosophila melanogaster*) have shown that both females (Partridge *et al.* 1986, 1987; Fowler and Partridge, 1989; Partridge and Fowler, 1990; Chapman, 1992) and males (Partridge and Andrews, 1985) permitted to mate with conspecifics of the opposite sex have reduced life expectancies compared with those of individuals of the same sex that are allowed to court but not to mate. The possible reasons for this differential mortality are still in debate but include mechanical injury, energetic consequences of courtship vigour, transfer of diseases or parasites, or some effect of sperm or accessory fluid (see, for instance, Partridge *et al.* 1986, 1987; Fowler and Partridge, 1989; Partridge and Fowler, 1990; Chapman, 1992).

For animals in which copulation is prolonged and/or frequent, one possible significant cost is an elevation of energy expenditure during mating. Recently Woods and Stevenson (1996) measured the energetic cost of copulation in the sphinx

moth (*Manduca sexta*), a species in which copulations are multiple, each taking approximately 3 h and in total accounting for approximately 3–15 % of the active portion of the 5 day life of a non-feeding adult. They concluded that the energetic costs of copulation in this species did not make a significant contribution to total energy demand. However, although copulation is prolonged in *M. sexta*, both sexes remain largely quiescent during mating (Woods and Stevenson, 1996).

In the tropical millipede *Alloporus uncinatus*, copulation involves physical restraint of the female by the male. Males control the duration of copulation, which is prolonged (several hours) under conditions of increasing male bias in the operational sex ratio (Telford and Dangerfield, 1990, 1991). In addition, our field observations (Telford and Dangerfield, 1993a) and laboratory mating experiments (Telford and Dangerfield, 1993b) confirm a polygynandrous mating pattern and suggest that individual males and females copulate repeatedly over the breeding season. In the present study, we estimate sex differences in the relative energetic cost of copulation in individual male and individual female *A. uncinatus* with the intention of assessing whether the energetic demands of copulation could represent a significant portion of total energy demand in this species.

Materials and methods

We selected 28 female and 28 male wild-caught *Alloporus uncinatus* (Attems) at random from communal single-sex

groups maintained in captivity at 22 °C under a natural photoperiod. All individuals were deprived of food for 24 h, weighed to the nearest 0.05 g, and then the resting oxygen consumption of each female (female standard metabolic rate, SMR) was determined over a 1 h period in Scholander respirometers maintained at 25 °C in a water bath. Copular pairs were then generated by introducing the females to the males, and each pair was randomly allocated to one of two experimental groups. In the first group, the oxygen consumption of each pair ($N=15$) was determined over a 1 h period, after which the female was killed by a lethal injection of 1 ml of ethyl acetate (the oxygen consumption of each of five control females during the hour immediately following injection with ethyl acetate was 0 ml, thus validating the efficacy of this method). In all cases, the male continued to copulate with the female even though she was dead. The oxygen consumption of the male plus the dead female was then measured over the subsequent hour and taken to represent the oxygen consumption of the male alone during copulation (male copular metabolic rate, CMR). Each pair was then separated, and the resting oxygen consumption of the solitary male (male SMR post-copulation) was measured over the following hour. For comparison, SMR was also determined in four males which had not copulated (male SMR pre-copulation). During copulation, the rate of oxygen consumption by the female (female CMR) was calculated as the difference between the rate of oxygen consumption by the copulating pair and male CMR.

In the second experimental group, pairs ($N=13$) were allowed to copulate for 1 h, after which the pair was separated and the resting oxygen consumption of the solitary female was determined over the following two 1 h periods (female SMR post-copulation). All values of oxygen consumption were converted to $\mu\text{l g}^{-1} \text{min}^{-1}$ at STP.

Results

Male SMR post-copulation did not differ significantly from male SMR pre-copulation (pooled variance $t_{17}=0.04$, $P=0.97$; Table 1). However, the lack of a difference should be treated with caution because of the large variation in male SMR pre-copulation (Table 1). Male CMR was significantly higher than male SMR post-copulation (paired-sample $t_{13}=20.4$, $P<0.001$), with oxygen consumption during copulation being elevated by $31.0\pm 1.5\%$ (mean \pm S.E.M., $N=15$; Table 1). Female SMR was significantly higher in both the first (paired-sample $t_{11}=12.6$, $P<0.001$) and the second (paired-sample $t_{11}=3.2$, $P=0.015$) hour after copulation than it was in the hour before copulation (Table 1). However, female CMR was significantly lower than female SMR pre-copulation (paired-sample $t_{13}=-3.7$, $P=0.005$) with the rate of oxygen consumption during copulation being depressed by $18.5\pm 5.6\%$ (mean \pm S.E.M., $N=15$; Table 1).

Discussion

Our data show an elevation in the rate of oxygen consumption by male *A. uncinatus* and a depression in the rate

Table 1. Rates of oxygen consumption before (SMR pre-copulation), during (CMR) and after (SMR post-copulation) copulation in male and female *Alloporus uncinatus* at 25 °C

	N	Mean ($\mu\text{l g}^{-1} \text{min}^{-1}$)	S.E.M.
Males			
Body mass (g)	19	8.74	0.14
SMR pre-copulation	4	1.173	0.209
CMR	15	1.541	0.035
SMR post-copulation	15	1.177	0.026
Females			
Body mass (g)	28	9.05	0.20
SMR pre-copulation (group 1) ^a	15	0.999	0.031
SMR pre-copulation (group 2) ^a	13	0.998	0.036
CMR	15	0.798	0.040
SMR post-copulation (first hour)	13	1.239	0.039
SMR post-copulation (second hour)	13	1.063	0.029

^aSee text for explanation of groups.

of oxygen consumption by female *A. uncinatus* during copulation. Once copulation had terminated, the rate of oxygen consumption of males rapidly returned to normal pre-copulation resting levels, while that of females was higher than normal pre-copulation resting levels for the following 2 h. These data are consistent with the build up of an oxygen debt during copulation by female, but not by male, *A. uncinatus*, this debt then being repaid once copulation is over. Other millipede species have been shown to incur an oxygen debt when subjected to conditions of low oxygen availability (for instance, in water-logged soil; Penteado and Hebling-Beraldo, 1991). During copulation in *A. uncinatus*, the coiling of the male around the female covers a significant number of her spiracles and this may suppress her ability to respire aerobically. If the post-copulation elevation in female SMR represents the repayment of an oxygen debt incurred during copulation, and that debt is fully repaid during the first 2 h post-copulation (see Table 1), then this implies that the metabolic rate (aerobic plus anaerobic metabolism) of the females during copulation was significantly elevated (pooled variance $t_{54}=2.04$, $P<0.05$) by $13.4\pm 6.0\%$ (weighted mean \pm S.E.M., $N=28$) above mean SMR pre-copulation across all 28 females ($0.998\pm 0.004 \mu\text{l O}_2 \text{g}^{-1} \text{min}^{-1}$; mean \pm S.E.M., $N=28$). The most obvious candidate for a short-term elevation in metabolic rate is increased muscular activity. The elevated metabolic rate of the females during mating suggests a certain resistance by females to prolonged copulation, with which there is presumably an associated risk of suffocation. The greater energetic costs incurred by males (a mean elevation of 31%) during copulation may have been due to the physical force required to subdue females. Mating in *A. uncinatus* appears to be size-selective, with females selecting males of approximately equivalent size to themselves. An indication of

the force exerted by the male during copulation is given by occasional decapitation of the female when there is an extreme mismatch in body size (Telford and Dangerfield, 1993a).

In contrast with *Manduca sexta* (Woods and Stevenson, 1996), these measured energetic costs of copulation in male and female *A. uncinatus* represent a significant energetic investment in reproduction, especially considering that individuals of both sexes could potentially mate in excess of 100 times over a 4 month breeding season (S. R. Telford, unpublished data). Additional potential costs of frequent remating are presumably a risk of suffocation for females if copulation is prolonged and the loss of time for both sexes which could otherwise be invested in maintenance activities (e.g. feeding). Female *A. uncinatus* often climb up vegetation, apparently to avoid potential sexual harassment from males searching for mates (Telford and Dangerfield, 1993a). In contrast, male *A. uncinatus* employ a random walk search tactic to locate potential mating partners, and field observations suggest that they are constantly active (Telford and Dangerfield, 1993a). It seems likely that this observed difference in behaviour between the sexes reflects a greater benefit of frequent mating (with multiple partners) for males than for females. Further support for this suggestion is provided by the physical restraint of the female by the male during copulation (although we have no way of telling whether the female is a willing participant). Also, it is males (not females, although females may not have the option) that extend the duration of copulation when the operational sex ratio is male-biased (Telford and Dangerfield, 1990, 1991). Such restraint presumably acts as a mechanism to prevent remating of the female by other males for as long as possible.

In summary, we found that there was a significant energetic cost of copulation in *A. uncinatus* and that this cost was higher for males than for females. Furthermore, the process of mate acquisition is also likely to be more energetically expensive for males. We suggest that other invertebrate species that have mating patterns typified by sexual harassment of females and frequent copulations involving physical restraint (Thornhill and Alcock, 1983) may incur similarly high costs. Such energetic demands of copulation are a previously overlooked cost of reproduction (Partridge and Andrews, 1985; Clutton-Brock, 1991) that could potentially represent a significant cause of reduced longevity.

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