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Effects of size at metamorphosis on stonefly fecundity, longevity, and reproductive success

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Abstract Many organisms with complex life cycles show considerable variation in size and timing at metamorphosis. Adult males of *Megarcys signata* (Plecoptera: Perlodidae) are significantly smaller than females and emerge before females (protandry) from two western Colorado streams. During summer 1992 stoneflies from a trout stream emerged earlier in the season and at larger sizes than those from a colder fishless stream, and size at metamorphosis did not change over the emergence period in either stream. We performed two experiments to determine whether variation in size at metamorphosis a ected the fecundity, reproductive success and longevity of individuals of this stonefly species and if total lifetime fecundity was a ected by the number of matings. In the first experiment, total lifetime fecundity (eggs oviposited) was determined for adult females held in small plastic cages in the field. Males were removed after one copulation, or pairs were left together for life and allowed to multiply mate. Most copulations occurred in the first few days of the experiment. Females in treatments allowing multiple matings had significantly lower total lifetime fecundity and shorter adult longevity than females that only mated once. Multiple matings also reduced longevity of males. Fecundity increased significantly with female body mass at emergence, but only for females that mated once. While multiple matings eliminated the fecundity advantage of large female body size, number of matings did not a ect the significant positive relationship between body mass at metamorphosis and longevity of males or females. In a second experiment designed to determine if body mass at emergence a ected male mating success, we placed one large and one small male *Megarcys* in an observation arena containing one female and recorded which male obtained the first mating. The large and the small male had equal probabilities of copulating with the female. Copulations usually lasted all night, and the unmated male made frequent, but unsuccessful attempts to take over the copulating female. Our data suggest that selection pressures determining body size at metamorphosis may operate independently on males and females, resulting in evolution of sexual size dimorphism, protandry, and mating early in the adult stage. We emphasize the importance of interpreting the fitness consequences of larval growth and development on the timing of and size at metamorphosis in the context of the complete life cycle.

Key words Drumming · Protandry · Sexual size dimorphism · Size at metamorphosis · Total lifetime fecundity

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Introduction

Variation in body size has fascinated naturalists for centuries (e.g., Darwin 1871; Mayr 1963). Some of the best documented examples of natural and sexual selection acting on body size have come from the study of organisms with complex life cycles (e.g., Bateman 1948; Collins 1979; Wilbur 1980; Thornhill and Alcock 1983; Werner 1986). Natural selection on females to maximize fecundity often results in larger body size, and thus, female-biased sexual size dimorphism (Istock 1981; Honek 1993; Head 1995), whereas sexual selection for large males often promotes male biased sexual size dimorphism (Fairbairn 1990). Conversely, smaller males or females may be favored in environments where risk of large-size-selective predation is high (Beck 1995) resulting in a trade-o between maximizing size and fecundity and minimizing predation (Forrest 1987; Berrigan and Charnov 1994; Smith and Van Buskirk 1995; Sparks 1996). Selection may also favor small males in sparsely distributed populations if small size facilitates mobility

and the ability to find and mate with more females (Ghiselin 1974). Optimal size at metamorphosis, therefore, occurs where the benefit:cost ratio is the highest (Forrest 1987).

Others have shown that variation in the timing of transitions between life history stages may have greater impact on fitness than size at metamorphosis (Semlitch et al. 1988; Rowe and Ludwig 1991; Twombly 1996; Zonneveld 1996). Timing of metamorphosis is under selection both to optimize the benefits of larval growth and minimize the costs of larval mortality. In organisms whose reproduction is constrained seasonally and size is related to fitness, both timing and size at metamorphosis are important (Rowe and Ludwig 1991). Thus, environmental variation in selection pressures operating on both larval and adult stages will influence the evolution of size and timing of emergence (e.g., Ludwig and Rowe 1990; Abrams et al. 1996; Werner and Anholt 1996).

Insects with terrestrial adults and aquatic larvae show considerable variation in size at metamorphosis (emergence), especially in the Hemimetabola (e.g., mayflies, Brittain 1990; stoneflies, Froehlich 1990; odonates, Anholt 1990). Most studies concerning the importance of size to aquatic insect performance have focused on interactions occurring during the larval stage (Peckarsky and Penton 1985; Peckarsky and Cowan 1991; Peckarsky et al. 1993), with relatively few studies on the e ects of size at metamorphosis on adult reproductive success (Anholt 1991; Flecker et al. 1988; Briegel 1990). Previous studies of stream-dwelling stonefly larvae have shown that size at metamorphosis may be influenced by larval intraspecific competition (Peckarsky and Cowan 1991), coexistence with drift feeding fish (Feltmate and Williams 1991) and timing of emergence (Hynes 1976; Moreira and Peckarsky 1994). Crowded stoneflies emerged at smaller sizes and had lower potential fecundities than stoneflies held at lower densities (Peckarsky and Cowan 1991). Feltmate and Williams (1991) suggested that predator-induced stress on larval stoneflies reduced size at emergence and lowered the potential fecundity of females. However, it is not known whether large size confers an advantage in terms of the reproductive success of males, or whether females that emerge at larger sizes can realize their potential fecundity.

Several life-history aspects of stoneflies suggest that size at metamorphosis may be a reasonable indicator of stonefly reproductive success in some species. Stoneflies have a relatively short adult reproductive phase compared to their long larval phase. In many species of stoneflies, the adults do not feed (Hynes 1976; Rupprecht 1990), making food acquisition and growth in the larval stage the primary determinant of adult size. Further, nutrients allocated to egg development and maturation are often acquired entirely during the larval stage (Brinck 1949). In contrast, for stonefly species that do feed as adults, egg maturation during the adult stage, timing of mating, and longevity of adult females may play a major role in determining reproductive success (Moreira 1993). Thus, we define potential fecundity for stoneflies as the number of eggs inside a female at emergence and realized fecundity as the number of eggs oviposited.

The objectives of this study were to determine the timing of emergence of a population of *Megarcys signata* (Plecoptera: Perlodidae) living in high altitude streams in western Colorado and to measure the e ects of size at metamorphosis on (1) male reproductive success, (2) female lifetime fecundity (number of eggs oviposited), and (3) the longevity of both males and females in the field. We also tested (4) whether multiple matings a ected fecundity or longevity. No previous studies have tested whether large males have a reproductive advantage in stoneflies. Although larger females have been shown to have higher fecundities at metamorphosis (Peckarsky and Cowan 1991), we sought to determine the relationship between potential fecundity and total lifetime fecundity. To meet these objectives we designed experiments to test the prediction that size at metamorphosis is a reliable indicator of individual fitness in stoneflies.

Materials and methods

Methods

Study sites

The study was carried out during the summer of 1992 at two stream sites in Gunnison County, western Colorado, United States. The East River site is third-order at 2940 m elevation, and Benthette Brook is a first-order tributary of the East River at 3040 m elevation. Both streams are cold water snowmelt streams that flow through the site of the Rocky Mountain Biological Laboratory. Benthette Brook is a shallow fishless stream bordered by willows and open meadows, whereas the East River is a deeper, faster-flowing trout stream with riparian vegetation consisting largely of willows and conifers. Although both streams have wide daily and seasonal fluctuations in temperature, the average temperature during this study was lower in Benthette Brook (Fig. 1).

Test organism

Experiments were carried out on a large predatory stonefly species, *Megarcys signata* (Perlodidae), common in fast flowing high elevation streams in western North America. Larvae grow rapidly throughout the autumn, overwinter as late instars and molt to their final instar by early summer (Allan 1982; Peckarsky and Cowan 1991). Final instars crawl out of the water and metamorphose under streamside vegetation or rocks. Males and females mate along the stream bank on logs or rocks, and females oviposit in the stream. Although drumming behavior (species-specific substrate-transmitted courtship signals) has been described for many stoneflies (Stewart and Maketon 1990; Moreira 1993), little is known about the mating behavior or drumming signals of *M. signata*.

Timing of emergence

Emerging adults were collected using slit emergence traps (Moreira and Peckarsky 1994) placed along the stream edge adjacent to ri es in both streams. Since previous studies reported *M. signata* to emerge at dawn (Peckarsky and Cowan 1991), traps were checked for newly emerged adults every day at 0800–0900 hours MDT. Size

at emergence was determined by weighing teneral adults using a Cahn C-31 microbalance. Stoneflies were chilled to reduce movement during weighing, placed in 250-mg gelatin capsules and weighed live. Head capsule width (HCW) and wing length (forewing) were also measured using a microscope with an ocular micrometer. A Kolmolgorov-Smirnov two-sample test indicated whether timing of emergence di ered between the sexes in either stream. Di erences between the two streams in body mass of newly emerged male and female stoneflies were analyzed using Student's *t*-tests. Seasonal trends in mass at emergence of males and females from the two streams were analyzed using general linear regression models.

Experiments

To ensure that only unmated stoneflies were used in experiments, we reared final instar female and male *Megarcys* in circular flow-through artificial stream chambers with natural mineral substrata (see Peckarsky and Cowan 1991). Larval stoneflies were provided unlimited food (their preferred prey, *Baetis bicaudatus*: Peckarsky and Penton 1989; Peckarsky et al. 1994) and maintained at one per chamber to reduce e ects of intraspecific competition on mass at emergence (Peckarsky and Cowan 1991). A Nitex mesh cover was placed over each chamber to prevent emerging adults from escaping and a small willow twig assisted final instars to climb out of the water. In experiments males and females were always paired with individuals from the same stream. Mass at emergence was determined using the same methods as those for teneral adults collected from the field emergence traps.

Male reproductive success experiment

To determine if mass at metamorphosis a ected male mating success, we placed one large (mean SE = 85.0 mg 2.73) and one small (53.0 mg 1.21) male of the same age (1 day) in a glass observation arena (45 × 22 × 25 cm) with a mesh top with a 1-day-old female (151.0 mg 4.21 SE). Because stoneflies use substrate-transmitted courtship signals, rocks, woody debris and willow twigs, typical substrates on which mating occurs, were placed in the arena. On the day they emerged, the two males were live-weighed, marked individually with non-toxic Speedball marker paint and then held in separate cages until late evening (2000–2100 hours). Their mating behavior was observed in arenas outdoors under a streamside tarp at night using dim red-light produced from standard incandescent headlamps covered with opaque red plastic. In the judgement of observers stonefly behavior was una ected by this artificial lighting. For 15 trials we recorded which male obtained the first copulation, noted its body weight, and also observed the behavior of the unmated male. A two-tailed chi-square test was used to determine whether mating success was random with respect to male mass at metamorphosis. Because of the experimental design this test assumes a constant di erence in size between males and that the mechanism of selection is based on the relative di erence in size rather than a threshold size.

Female lifetime fecundity experiments

Unmated stoneflies from both streams obtained from the rearing chambers were weighed as above and placed in smaller plastic cages (20 × 14 × 11 cm) also located under the streamside tarp in the field, provided with 10% sugar solution for food, a small dish of water in which females could oviposit, a rock and willow twig for shelter and mating substrata. Treatments were allocated randomly to pairs of stoneflies to determine the e ects of the number of matings and mass at emergence on female total lifetime fecundity and longevity of males and females. Males and females were always paired with individuals from the same stream. In the first treatment, a male/female pair was placed in each of 20 cages and observed until the first copulation, at which time the male was removed and both were held in separate cages until they died. In the second treatment, 20 male/female pairs of stoneflies were held together in cages until death, thus, given the opportunity for multiple copulations. In a third treatment, 20 virgin females were placed in similar cages without males and held until death to determine if unmated females would oviposit viable eggs (parthenogenesis).

In all experiments, cages were checked periodically throughout the day and after dark for copulating pairs, and total lifetime fecundity for females in each treatment was determined by counting all eggs oviposited by each female over her lifetime. Date and time of death were recorded for all individuals and at the end of the experiment females were dissected to determine the number of immature eggs remaining at death. E ects of number of matings on total lifetime fecundity and longevity were analyzed by ANOVA, and analysis of covariance determined whether number of matings a ected the relationship between body mass at emergence and total lifetime fecundity or longevity.

Results

Timing and mass of *Megarcys* at emergence

In 1992 *Megarcys* began emerging from the East River in mid-June, peak emergence was in late June and continued until mid-July; whereas the population of *Megarcys* in Benthette Brook was displaced by almost a month, with the onset of emergence in early July, peak in late July and end in late August (Fig. 1). During most of the summer adults emerged at dawn (0600–0800 hours), but later in the season *Megarcys* often emerged at night (after 2200 hours) in both artificial stream tanks and in the field. Males and females emerged in equal numbers (1:1 sex ratio) during peak emergence, and male *Megarcys* emerged significantly earlier than females (protandry) in both streams (KS tests, East River: $P = 0.00127$; Benthette Brook: $P < 0.001$, Fig. 1), as is typical of stoneflies (Harper and Pilon 1970; Hynes 1976). A similar pattern was reported by Peckarsky and Cowan (1991) in studies of *M. signata* reared in artificial stream tanks.

Mature *Megarcys* larvae (determined by well-developed wing pads) were observed close to the water's edge on the underside of rocks. Mature female larvae, which cease feeding just before emergence, were generally aggregated, while mature males, which males continue to feed (Peckarsky and Cowan 1991), were rarely found in close vicinity to one another. No aggregations of adult males or females were observed. Adults were primarily found alone or in pairs under rocks, dead logs or any other objects that provided shelter. Adults held in experimental cages showed behavioral periodicity similar to that of the larvae (Peckarsky and Cowan 1995) becoming increasingly active just after dusk.

A distinct sexual size dimorphism was observed for *Megarcys* in both streams, with females attaining about twice the body mass of males at metamorphosis (mean SE body weight in mg: East River females: 159.8 5.49, $n = 45$; males 69.9 1.47, $n = 59$; Benthette Brook females 112.9 2.99, $n = 73$; males

53.8 1.36, $n = 40$). This pattern is common in many other stoneflies with short-lived non-feeding adults (e.g., Perlidae: Moreira 1993; Perlodidae and Chloroperlidae: Harper 1973).

There was considerable variation in size of males and females emerging throughout the summer, but size at metamorphosis did not decrease throughout the emergence period (Fig. 2). *Megarcys* from the trout stream (East River) emerged at larger sizes than those in the colder fishless stream (Fig. 2, females: Student's $t = 8.164$, $P < 0.001$, 115 *df*; males: Student's $t = 7.598$, $P < 0.001$, 96 *df*). Females from the trout stream also had longer wings than females from fishless stream, many of which were brachypterous (short-winged). Temperature increased during the summer in both streams, but the average temperature was higher in the East River (Fig. 1, mean SE temperature in °C: East River: 7.3 0.17; Benthette Brook: 6.1 0.10).

Male reproductive success experiment

There was no e ect of body mass on male reproductive success in our experiments. Of the 15 pairs of males tested, the large male copulated successfully 8 times and the small male 7 times ($\chi^2 = 0.066$, $P > 0.05$, 1 *df*). Thus, under these conditions, mating was random with respect to male size at emergence.

Male *Megarcys* exhibited courtship drumming signal behavior on the mesh lids of observation arenas during these experiments. Activity of both males and females increased dramatically just after dark, when they began to move rapidly about the chambers eventually crawling up the glass sides or willow twigs onto the mesh-covered top where males would vibrate their abdomens. In some trials when the female detected these vibrations, she moved quickly to the signaling male and copulated immediately. That sequence of male and female behaviors

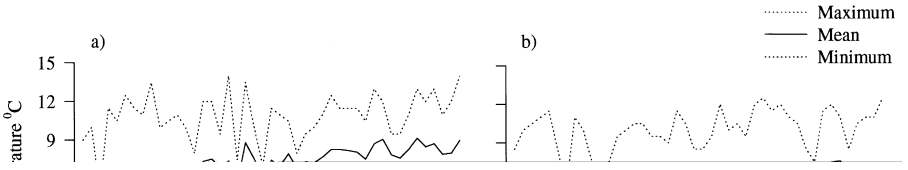

Fig. 1 Water temperature (°C) and numbers of adults emerging of *Megarcys signata* in a East River and b Benthette Brook. Emergence data from daily samples are grouped at 3-day intervals. Protandry (males emerge first) is significant at both sites (Kolmolgorov-Smirnov test)

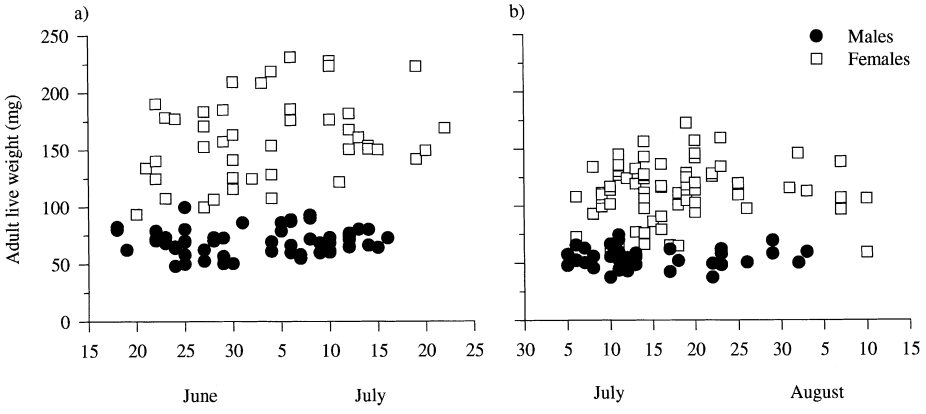

Fig. 2 Size of male and female *Megarcys* emerging over time from a the East River and b Benthette Brook. Regressions between time and size at metamorphosis were not significant. East River males: $r^2 = 0.006$, $P > 0.05, n = 58$; females: $r^2 = 0.071, P > 0.05, n = 44$; Benthette Brook males: $r^2 = 0.002, P > 0.05, n = 40$; females: $r^2 = 0.002, P > 0.05$, $n = 73$

is not typical of most stonefly species (Stewart and Zeigler 1984), in which males actively search for females after they exchange drumming signals (Moreira 1993). In other trials, the first male to contact the female mated with her, while the unmated male would eventually locate the copulating pair and attempt to dislodge the other male. Copulations generally lasted all night (maximum 11 h), with the unmated male making frequent, but unsuccessful attempts to take over the copulating female, and often attempting unsuccessfully to insert his genitalia into the female. Therefore, in our experiment the first male to drum on the mesh surface or to locate the female was successful, independent of body mass at metamorphosis.

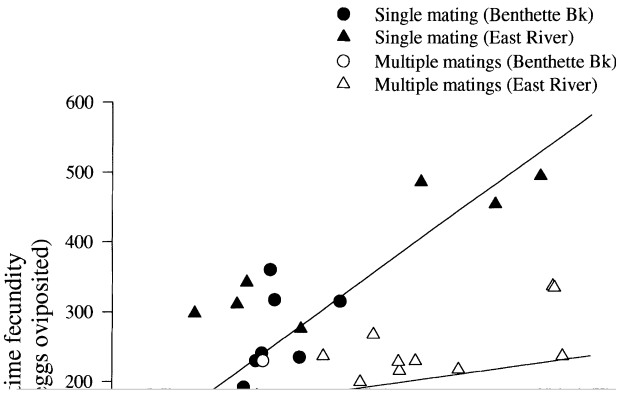

Fig. 3 E ect of size at metamorphosis on number of eggs oviposited per female by *Megarcys* from the East River (*triangles*) and Benthette Brook (*circles*), allowed one (*closed symbols*) or multiple (*open symbols*) matings. Slope of regression for body weight vs. fecundity for females with single matings is significantly di erent than zero ($y = 0.791x - 165.6, r^2 = 0.626, P = 0.00003, n = 20$). Slope of regression for body weight vs. fecundity for females with multiple matings is not significantly di erent than zero ($y = 0.291x + 93.32, r^2 = 0.085, P = 0.212, n = 20$)

Female lifetime fecundity experiment

Female *Megarcys* subjected to multiple matings had significantly lower total lifetime fecundities (ANOVA, $F = 52.04$, $P < 0.001$; 2, 56 *df*), demonstrating a potential fitness cost to females of multiple copulations (Fig. 3). Dissection of the reproductive tracts of 25 females chosen randomly from treatments after they had oviposited and died showed that females of all sizes had negligible numbers of undeveloped eggs remaining. Multiple matings also reduced the adult longevity of both females and males (Fig. 4, ANOVA, $F = 72.75$, $P < 0.001$, 2, 57 *df*; $F = 7.47$, $P = 0.0013$, 2, 58 *df* respectively). Unmated females lived the longest (mean = 24 days), but rarely oviposited providing no evidence for parthenogenesis in this species.

Total lifetime fecundities increased significantly with increasing female body mass at emergence, but only when females mated once (Fig. 3, ANCOVA, significant treatment e ect: $P = 0.034$, size e ect: $P < 0.001$ and interaction between treatment and size on fecundity: $P = 0.0015$). Multiple matings eliminated this large size fecundity advantage, with the slope of the body size versus fecundity regression line not significantly di erent than zero (Fig. 3). Egg size was relatively invariant compared to the observed variability in egg numbers and did not covary with female body weight (Peckarsky and Cowan 1991; B.L. Peckarsky, unpublished work). Females and males rarely fed on the sugar water at any time in our experiments (only two females). Dissections of adult *Megarcys* collected in the field revealed atrophied digestive tracts suggesting that this species does not feed as adults.

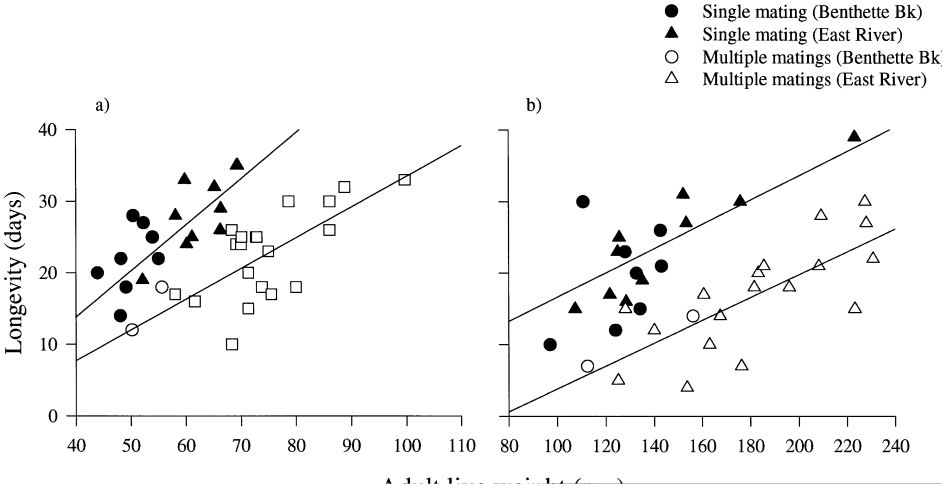

Fig. 4a, b E ect of mass at metamorphosis on longevity (time from emergence until death) for *Megarcys* males and females from East River (*triangles*) and Benthette Brook (*circles*). Slopes of regressions for body weight vs. longevity for a males and b females with single (*closed symbols*) or multiple matings (*open symbols*) are significantly different from zero (males with single matings: $y = 0.753x - 11.93, r^2 = 0.568, P = 0.00013, n = 20$; males with multiple matings: $y = 0.672x - 9.48, r^2 = 0.452, P = 0.00117, n = 20$; females with single matings: $y = 0.706x - 0.273, r^2 = 0.449, P = 0.005, n = 20$; females with multiple matings: $y = 0.773x - 12.12, r^2 = 0.597, P = 0.00007, n = 20$)

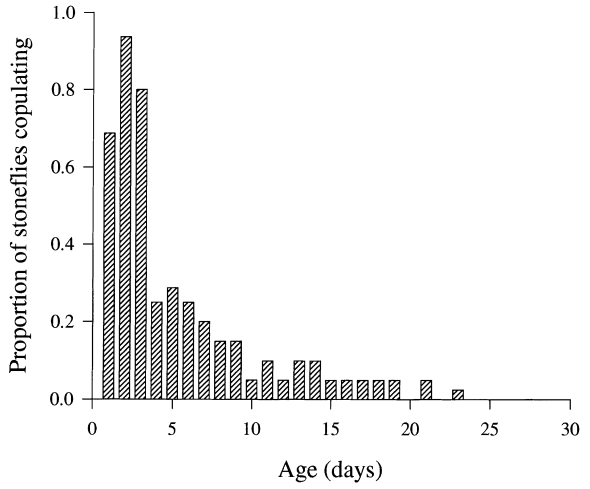

Fig. 5 Age at first reproduction for *Megarcys* in experimental enclosures

Adult longevity also increased significantly with increasing body mass at emergence for male or female stoneflies, (ANCOVA, significant size e ect, $P < 0.001$ for both males and females); and this relationship was una ected by numbers of matings (Fig. 4, ANCOVA, no significant treatment e ect, $P = 0.145$, $P = 0.830$, females and males, respectively) or interaction between treatment and size e ects on longevity ($P = 0.846$, $P = 0.227$ for females and males, respectively). The longevity of females ranged from 4 to 39 days at ambient temperatures, with an average life span of 18 days. Males, on average, lived slightly longer, up to 35 days when unmated, with an average life span of 24 days. We suspect that this relatively long life span is rarely achieved under natural field conditions where predation pressure may be intense. Interestingly, the first copulation occurred very early in the adult stage, mostly within the first 3 days after emergence (Fig. 5). Further, we found that whenever newly emerged males and females encountered one another in the field emergence traps, they would copulate. A maturation period, required by other stoneflies before they are receptive or will drum (Moreira 1993), is apparently not necessary for *Megarcys*.

Discussion

The size as well as timing of metamorphosis of organisms with complex life cycles must balance the benefits of extended larval growth to maximize size and fecundity, with the costs of delaying reproduction or increasing risks of predation (Semlitch et al. 1988; Rowe and Ludwig 1991; Twombly 1996; Zonneveld 1996). Further, selection pressures determining body size at metamorphosis may operate independently on males and females, depending on the relative costs and benefits of attaining large body size (Kleckner et al. 1995). For example, selection may favor small adult males and large adult females, and those selection pressures may operate to shape behaviors occurring in the larval stage (Prout and McChesney 1985).

Our data show that there was considerable variation in size at metamorphosis, but that this was not a function of timing of emergence. Variation in temperature has been proposed to explain this pattern, where increased metabolic costs at higher water temperatures result in decreased sizes at metamorphosis as water temperatures warm (Sweeney and Vannote 1978). However, this hypothesis is often not supported by observed field patterns. For instance, Sweeney et al. (1995) observed a seasonal decrease in size at emergence in mayflies that emerge from a tropical stream where temperature is fairly constant. In addition, Forrest (1987) and B.L. Peckarsky (unpublished work) found that only one generation of a bivoltine species decreased in size throughout emergence while the other did not. Our study provides no evidence that temperature-mediated di erences in developmental rate a ected body size in either stream. Our data suggest that with respect to size at metamorphosis there is little cost to delaying emergence.

In contrast, timing of metamorphosis can influence factors other than body size that may be costs or benefits depending upon the life stage. For organisms such as *Megarcys* that feed primarily as larvae delaying timing of metamorphosis enables individuals to increase in size prior to metamorphosis, which, for females often translates into higher fecundity, but carries with it the costs of delaying reproduction (Rowe and Ludwig 1991). Although *Megarcys* emerged over a 2-month period in our study emergence was skewed toward early in the season. If lethal and sublethal costs such as predation or parasitism are high in the larval or adult habitat later in the season then selection will favor emerging early. Further, in terms of mating success emerging early may allow males and females more time to locate a potential mate, especially in species that are sparsely distributed (Ghiselin 1974) and have complex mate finding behavior as in stoneflies (Stewart 1994). The influence of timing of metamorphosis on mate searching and adult mortality caused by predators o ers a fruitful area of further research.

Our study provided no evidence of a large male advantage in *M. signata*, suggesting that the benefits to males of achieving large body size may not exceed the costs. In males, body size contributes very little to gamete production, since sperm are energetically ''cheap'' and a superabundance can be produced by either a large or a small male. In species where males transfer nutrients in their semen (via spermatophore), selection may favor larger males capable of donating more nutrients (Boggs 1990). However, there is no evidence of spermatophore production in this or any other species of Plecoptera. On the other hand, larger individuals may be more vulnerable to predation (as larvae or adults), and loading constraints during long copulations may also favor small male size. In stoneflies the male copulates with his head

and thorax on top of the female and his abdomen twisted beneath her, and females carry males in this position for extended periods of mate guarding. Thus, loading constraints may promote the evolution of sexual size dimorphism (Adams and Greenwood 1987; Naylor and Adams 1987; Fairbairn 1993) with females larger than males. Further, body size may reflect optimal energy allocation to mating (Thornhill and Alcock 1983) or mate guarding (Zeigler 1991) in organisms with size-assortative mating (Thornhill and Alcock 1983). Thus, both sexual selection and natural selection may operate concurrently to determine optimal male body size (Lande 1980).

Our data suggest that factors other than body size, such as e cient mate search strategy were the most important to male reproductive success (Parker 1982; Zeigler 1990, 1991; Abbott and Stewart 1993; Stewart 1994; Kotiaho et al. 1996). If adults are short-lived, sparsely distributed during emergence, and do not form mating aggregations (swarms), then mating with the first male encountered may be the optimal strategy for females, especially if the costs of locating other males and making comparisons are high (Wittenberger 1983). Under natural conditions predation and poor flight ability could make finding mates di cult, and waiting for a more fit mate may be a suboptimal strategy for *M. signata* females. Since the habitat in our observation chambers may not have provided opportunities for size-related variation in male search e ciency that could occur in nature, our conclusion that male body size is unimportant to reproductive success must be tentative. Careful studies of the drumming signals of this species will elucidate its role in male mating success and determine whether variation in courtship success is a function of body size.

In contrast, our data provide strong evidence of a large female advantage (increased fecundity) for *M. signata* suggesting that natural selection favors larger females. Previous studies of this and other species of stoneflies have shown that female body size was correlated with potential fecundity, or numbers of eggs present at emergence (Peckarsky and Cowan 1991; Moreira 1993). In our experiments this positive relationship between female body size and potential fecundity was reflected in total lifetime fecundity under conditions where females mated only once. Thus, in this and other species with short-lived or non-feeding adults (e.g., mayflies) that produce all their eggs as larvae, fecundity at emergence may be a reasonable predictor of total lifetime fecundity (Istock 1967). Even in species with longer-lived and feeding adults, energy or fat acquired during the larval stage may be stored and used for maintenance and egg production or maturation in the adults (Zwick 1973; Marden 1989).

The observed decrease in fecundity and longevity for females that received multiple matings may indicate stress caused by remittent copulations, which has been shown to lower longevity in female stoneflies of another species (Moreira 1993) and other insects (Rowe et al. 1994). Our data further demonstrate that events occurring in the adult life stage can counteract the potential advantage of achieving large body size as a larva. The influence of the adult stage on realized fecundity increases in species with longer-lived adults that feed (e.g., odonates and some stoneflies; Marden and Waage 1990; Anholt 1992; Moreira 1993). Thus, number of eggs oviposited over the lifetime of the female, as measured in this study, along with measures of egg quality and hatching success are perhaps the best predictors of female fitness, taking into account processes a ecting the complete life cycle (Leather 1988).

The large female advantage, negative e ects of multiple matings on total lifetime fecundity and longevity, and the observation that most matings took place in the first few days of the experiment suggest that natural selection promotes female-biased sexual size dimorphism, protandry and early age of reproduction. Size di erences may also be the result of intraspecific di erences in number of instars for each sex, such that male development time is less (Sephton and Hynes 1982), resulting in early male maturation, protandry (Banghman 1992) and smaller male size. In both streams males emerged before females, as reported previously in experimental chambers (Peckarsky and Cowan 1991) and field studies (Cather and Gaufin 1975). Evolution of protandry (reviewed by Wiklund and Fagerstrom 1977; Wiklund and Solbreck 1982; Bulmer 1983) generally results from selection on independent fitness criteria for each sex (Kleckner et al. 1995). For example, selection for large females may delay emergence, while selection for smaller males might accelerate development and lead to earlier metamorphosis. Protandry might also reduce prereproductive deaths of either sex by facilitating rapid fertilization for insects having short-lived adults with a limited time to reproduce (Richards 1927).

Drumming courtship behavior of stoneflies has been proposed as another possible mechanism favoring early emergence of males. Moreira (1993) showed that males of a perlid stonefly took several days (6 days) to mature before they were able to produce a high quality drumming signals (assessed by responses of females to playback experiments). This male maturation period corresponded with the magnitude of protandry. Although *M. signata* had a similar mean age of first copulation (4 days), some 1-day-old males mated successfully without drumming, suggesting that neither drumming nor extended male maturation after metamorphosis were obligate for mating to occur in this species. However, in more complex natural mating habitat of this species in the riparian zone of streams drumming may play a more important role in the location of mates.

Summary and considerations for future study

In conclusion, our data demonstrate that di erent selection pressures may be operating on male and female

stoneflies in both the larval and adult stages that a ect the timing and size of individuals at metamorphosis. We suggest that more attention should be paid to factors a ecting realized fecundity rather than potential fecundity, since natural mortality may prevent most individuals from achieving their potential fecundity. The positive female size at metamorphosis: fecundity relationship may be confounded by events occurring in the adult stage and should be tested directly before inferring fitness consequences of size variation within and between populations of larvae. Although mating behaviors and size variation of males and females provide opportunity for sexual selection in stoneflies, their role remains to be determined directly. Our data suggest that male size does not a ect reproductive success, although other factors such as male age or mate searching e - ciency may be important. Mating occurs early in the adult phase, reflecting a potential constraint of high mortality on mate finding in free-ranging adults. Clearly, more studies are needed to understand the consequences of larval growth and development on the adult reproductive performance of organisms with complex life cycles.

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