# No size-dependent reproductive costs in male black scavenger flies (*Sepsis cynipsea*)

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Mating is generally assumed to be costly, but mating costs differ between the sexes. Although mating itself is considered cheaper for males, mate search and mate competition are cheaper for females. Nevertheless, studies increasingly reveal considerable mating costs for males, and these costs should depend on the body size of the individual. We investigated size-dependent predation (ecological) and energetic (physiological) mating costs in male black scavenger flies, *Sepsis cynipsea* (Diptera: Sepsidae), a model organism for studies of reproductive behavior. We addressed costs of mating by assessing predation risk for differently sized flies in male, female, and mixed-sex groups. Males were not more likely to be predated in mating or mate-search situations. *Scathophaga stercoraria* (Diptera: Scathophagidae) predators preferred smaller females and males as prey. Male movement in these different social situations does not proximately explain this size-selective predation, as small individuals were not more mobile. We addressed energetic costs of mating by measuring residual longevity (or starvation resistance) of starved males exposed to different mating situations. Copulation, courtship, interaction with reluctant females, or brief interactions with other males, all presumably increasing energy demand, did not significantly reduce longevity of males compared with males not interacting with other individuals. In general, small males died sooner when starved. Overall, we found no direct costs of mating for male *S. cynipsea*, but both predation and physiological costs were size dependent. *Key words:* body size, energetic costs, food limitation, mating behavior, mortality, predation, starvation resistance. *[Behav Ecol 21:85–90 (2010)]*

Reproduction is generally assumed to be costly. These costs include the physiological costs of producing gametes and associated products, the cost of mating itself, and the investment in offspring (Daley 1978; Calow 1979). Direct costs of mating have been found to be a reduced life span (Fowler and Partridge 1989; Gems and Riddle 1996; Chapman et al. 1998; Stutt and Siva-Jothy 2001; Yanagi and Miyatake 2003; Pakku and Kotiaho 2005), injuries (Crudgington and Siva-Jothy 2000; Blanckenhorn et al. 2002), toxins (Chapman et al. 1995), parasites or diseases transmitted during mating (Sheldon 1993), lost time or energy (Arnqvist 1989; Watson et al. 1998), and higher predation or parasitism risk (Gwynne 1989; Magnhagen 1991; Rowe 1994; Pocklington and Dill 1995). Further, indirect costs associated with mating are lost time and energy and a higher predation risk when searching (Slagsvold et al. 1988; Magnhagen 1991; Gibson and Langen 1996), attracting (Lima and Dill 1990; Magnhagen 1991; Cordts and Partridge 1996; Kotiaho et al. 1998; Zuk and Kolluru 1998), assessing (Pomiankowski 1987; Hedrick and Dill 1993; Reynolds and Côté 1995), or rejecting potential mates (Rowe 1994; Watson et al. 1998; Jormalainen et al. 2001).

Costs of mating typically differ between the sexes (Brower and Calvert 1985; Gwynne 1989; Pocklington and Dill 1995; Gems and Riddle 1996; Jormalainen et al. 2001). Predation risk, for example, has been found to be greater for the sex attracting mates via acoustic or visual signals or for the sex that has to move farther to find mates (Lima and Dill 1990; Magnhagen 1991; Zuk and Kolluru 1998). The sex competing for mates, typically males, frequently endures costs such as lost energy or injuries (Andersson 1994). In contrast, greater costs

of gamete production and of mating itself are usually attributed to females (Bateman 1948; Trivers 1972; Arnqvist and Nilsson 2000), although in species with nuptial feeding males may invest as much or more in matings than females (Simmons 1993; Vahed 1998). To better understand sexual conflict and its outcome, it is important to understand the relative costs of different aspects of reproduction for both sexes.

Costs and benefits of mating also differ within the sexes depending on individual characteristics such as body size or condition. Larger individuals in good condition often win intrasexual conflicts or are favored by mate choice (Andersson 1994). Larger females in good condition typically produce more offspring (Roff 1992; Honek 1993; Andersson 1994), and larger males often transfer larger ejaculates or sperm at higher rate (e.g., Simmons and Parker 1992; LaMunyon and Eisner 1994). Moreover, predation risk has been found to depend on body size because of size-selective predators (e.g., Wellborn 1994; Berger et al. 2006; Mand et al. 2007). Individuals therefore likely differ in their optimal investment in various aspects of mating depending on their size or condition (e.g., Gwynne 1990; Blay and Yuval 1997; Dunn et al. 1999).

Reproductive behavior has been investigated extensively in the black scavenger or dung fly *Sepsis cynipsea*, a small, ant-like fly that lays its eggs into cow dung. The mating system is characterized by scramble competition of males for females on and around fresh cow pats. Direct male–male aggression is rare. Females are guarded by males during egg laying and copulate only afterward in about 40% of the cases (Parker 1972; Ward 1983; Ward et al. 1992). Females unwilling to mate perform conspicuous shaking behavior. Large males regularly have a mating advantage (Ward 1983; Blanckenhorn et al. 1999, 2000, 2004). Costs of mating have been identified in both sexes. Although females that copulated more often or were held with males died sooner and accumulated more wing injuries than females held with other females, males held with other males had the lowest survivorship and most

wing injuries (Blanckenhorn et al. 2002; Mühlhäuser and Blanckenhorn 2002). Shaking behavior of reluctant females appears to be energetically costly and time consuming, at least for females, as indicated by females shaking less when harassed by more males (Blanckenhorn et al. 2000). Mating per se does not appear to increase predation risk; instead, males were found to have greater predation risk than females when held in all-male groups, presumably because males are then more active in search of females (Mühlhäuser and Blanckenhorn 2002). However, in all these studies, any possible body size dependence was not addressed.

Here, we assess potential size-dependent mating costs for male *S. cynipsea* in more detail with a series of laboratory experiments. We performed laboratory predation experiments using differently sized flies. We additionally assessed the movements of differently sized males in an attempt to link their higher mortality to their behavioral conspicuousness to potential predators. Finally, we investigated the fitness consequences of the energetic costs of shaking and copulation for males in terms of reduced life span by starving males with different mating histories.

## MATERIALS AND METHODS

### General methods

Flies used in this experiment stem from laboratory cultures held under standard conditions at 25 °C, 60% humidity, and 12-h light period with sugar, pollen, and water ad libitum and fresh cow dung for egg laying (for more details see Blanckenhorn et al. 2000). To initiate laboratory cultures, flies were collected in summer (May–August) each year on a cow pasture in Fehraltorf, near Zürich, Switzerland. To assure that females were virgins, flies were separated by sex within 24 h after emerging and kept in single-sex containers with water, sugar, pollen, and cow dung.

### Size-dependent predation

To test size-dependent predation risk, we set up single-sex and mixed-sex groups of flies with variable body size. We tested 10 replicate all-male, all-female, and mixed-sex groups (each). Sixteen large, 16 medium-sized, and 16 small flies aged approximately 1 week were assigned to each 3.5-l container; in mixed-sex containers, half of each size class were males and half females. Size class was determined by eye; left hind tibia length of all flies was measured at the end of the experiment using a binocular microscope at ×40 magnification. In the test containers, flies were provided with water, sugar, pollen, and 50-g fresh cow dung; a fresh plant leaf in a small water jar was added as potential shelter.

Sepsid flies were moved to their test containers in the afternoon and kept in a climate chamber at 25 °C and 60% humidity. The next morning, the most common predator around fresh cow dung in Switzerland was added, a hungry female yellow dung fly (*Scathophaga stercoraria*) that had been provided with sugar for energy but not with prey necessary to reproduce. Forty-eight hours later the experiment ended, and we checked whether *Sepsis* flies had been eaten or died otherwise (as distinguished by bite marks), and tibia length of all flies was measured (see Mühlhäuser and Blanckenhorn 2002 for details). The head width of the predators was also measured.

A total of 10 replicate groups per treatment were tested. Proportions were arcsine square-root transformed. For each group, the body sizes ($X$) were first z-scored, $z_i = (X_i - \text{mean}(X))/\text{SD}(X)$; the selection differential is then simply the mean standardized body size of the surviving flies.

### Size-dependent male movement

To estimate the movements of males, a grid was drawn on hexagonal (cross section) 3.5-l plastic containers; each of the 6 sides of the container measured 8 × 18 cm and was subdivided into 12 equally sized rectangles. During 1 h, every movement from 1 rectangle to the next was recorded and counted as 1 movement unit. Twenty males aged 4–12 days post emergence were tested in each of 4 different treatments on 3 consecutive days. We covered a large body size range. 1) The first day males were tested alone with sugar, pollen, and water only. 2) After this trial, 5 large and 5 small males (size was judged by eye) of the same age were added, and the next day, after habituation overnight, the movements of the test male were scored again. 3) Afterward, a 10-g portion of fresh dung was added, and male behavior in this new situation was recorded for another hour. 4) The following day, fresh dung and 11 females (to produce a 1:1 sex ratio) were added, and the movements of the target male were scored for the last time. At the end, head width of all males and females was measured. The wings of target males were painted with red and the wings of all other males with green color, whereas females were not marked at all.

### Size-dependent longevity costs of mating

Two hundred and fifty males, all 5–6 days old, were assigned to 8 different treatments. 1) "Four copulations": Males received the opportunity to copulate 4 times on 1 day. Females reluctant to mate were exchanged. As not all males copulated 4 times, the actual number of copulations was recorded. 2) "Four copulations + rest": As before males had the opportunity to copulate 4 times; afterward, they were moved singly into 50-ml glass vials with sugar, pollen, and water ad libitum, where they could rest at 25 °C for 1 day. 3) "2 + 2 copulations": Males had the opportunity to copulate 2 times on 1 day, then rested overnight alone with water, sugar, and pollen ad libitum, whereafter they could copulate another 2 times the following day. 4) "One copulation": Males copulated with 1 female only. 5) "Shaking": a female that had copulated the day before and therefore most probably would be reluctant to mate (i.e., shake off the male) was presented to the males. Only pairs that shook but did not copulate were used in the end. 6) "Male pairs": Males often jump on the back of each other, but then they do not shake like females, so interactions are brief. Two males were placed together in a test vial for 20–45 min for as long as a typical copulation (in groups 1–4) lasts. Then males were exchanged, until each male had had 4 male partners. 7) "Males alone (control 1)": Males were kept alone in test vials without sugar and water for the duration of a typical copulation (in groups 1–4). 8) "Males from holding container (control 2)": Males were taken without any treatment directly from the holding container. After their respective treatments, males were kept singly in 50-ml glass vials, provided with water only in a cool, 12 °C climate chamber (to stretch their life span) until they died. We checked 3 times per day for dead flies.

Four supplementary treatments were performed to test for mass container effects. 9) Similar to control 2, males from the holding container were directly moved to 12 °C. 10) Males from the holding container were moved singly to 50-ml glass vials with sugar, pollen, and water ad libitum for 3 days at 25 °C. 11) As in control 1, males were kept during the day without sugar and pollen, but then in the evening moved into 50-ml glass vials with sugar, pollen, and water ad libitum for 2 days at 25 °C, or 12) they were moved into 3.5-l mass containers with sugar, pollen, and water ad libitum for 2 days at 25 °C. As for treatments 1–8, males of all these 4 supplementary treatments 9–12 were at the end moved on the same day into 50-ml vials with only water into a 12 °C climate chamber until they died.
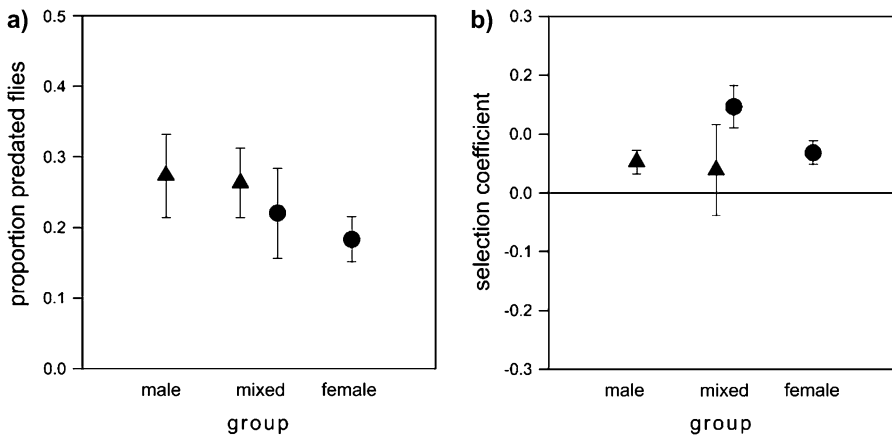
**Figure 1**
Predation of yellow dung fly females on *Sepsis cynipsea*: (a) proportion ± standard error (SE) of predated flies, (b) selection differentials ± 95% confidence interval of size-selective predation in all treatments (all-male, all-female, and mixed-sex group). Males are represented as triangles and females as circles.

Head width of all males tested was measured using a binocular microscope with $\times 40$ magnification.

## RESULTS

### Size-dependent predation

The proportion of surviving flies did not differ between male, female, and mixed-sex containers (analysis of covariance [ANCOVA] with predator size and mean *Sepsis* size of each group as covariates and treatment as a factor: $F_{2,29} = 1.23$, $P = 0.31$; Figure 1a). Within mixed-sex containers, the proportion of surviving males and females also did not differ (paired *t*-test: $t_9 = -0.585$, $P = 0.573$; Figure 1a). Larger predators ate more prey (predator-size effect: $F_{1,29} = 16.79$, $P < 0.001$).

Independent of sex, in all treatments, small flies were more likely to be predated (one-sample *t*-test testing the selection differential of each container against zero; all treatments: $t_{28} = 5.71$, $P < 0.001$; separated by treatments: all-male $t_9 = 2.51$, $P = 0.033$; all-female $t_9 = 3.37$, $P = 0.008$; mixed $t_9 = 4.00$, $P = 0.004$; Figure 1b). That is, selection differentials were on average positive (mean selection differential $+/-$ SE (standard error) for females = $+0.049 \pm 0.015$; for males = $+0.045 \pm 0.017$), so larger flies survived better.

### Size-dependent male movement

Males appeared to move more in all-male groups (with or without dung) than when alone or in mixed-sex groups (Figure 2). When females were present, males tried to copulate and stayed in the same place for a longer time, either in copula with a female or on her back. However, all these differences were not significant (repeated-measures analysis of variance with male size as covariate: $F_{3,54} = 1.27$; $P = 0.294$), and small males did not move more than large males ($F_{1,18} = -0.07$; $P = 0.793$; Figure 4a).

### Size-dependent longevity costs of mating

When testing young, virgin males (treatments 1–8), residual longevity in the 12 °C climate chamber varied significantly among treatments ($F_{7,212} = 11.64$; $P < 0.001$, ANCOVA with treatment as fixed factor and size as covariate; Figure 3a). Larger males tended to live longer ($F_{1,212} = 2.86$; $P = 0.092$; partial correlation $r = 0.11$). The overall variation in residual longevity between treatments was entirely due to longer survival in treatments 2 and 3, the 2 treatments in which males could rest after copulation (Figure 3a): When excluding these 2 treatments, residual longevity no longer varied among treatments ($F_{5,171} = 1.59$; $P = 0.165$). To test whether the actual

number of copulations influenced residual longevity independent of treatment, it was used as a covariate instead of treatment in those treatments in which males could not rest after copulation. However, the number of copulations had no effect on residual longevity (multiple regression: $F_{1,172} = 0.06$; $P = 0.803$).

When testing older, mass-held males (treatments 9–12), residual longevity differed significantly between the 4 treatments (ANCOVA with treatment as factor and body size as covariate: $F_{3,103} = 11.6$; $P < 0.001$; Figure 3b). Males kept nearly 6 h without sugar and moved afterward into mass containers (treatment 12) apparently could not restore their reserves fully there and had the shortest life spans (Figure 3b). Males that were kept 2 days alone with food ad libitum survived longest, independent of the treatment before (treatments 10 and 11; Figure 3b). Body size did not influence longevity ($F_{1,103} = 2.74$; $P = 0.101$), but its effect was in the same direction as in treatments 1–8 (partial correlation $r = 0.15$). When combining all the data of treatments 1–12, larger males survived longer (ANCOVA with treatment as factor and body size as covariate: $F_{1,316} = 30.26$; $P = 0.022$; partial correlation $r = 0.12$; Figure 4b).
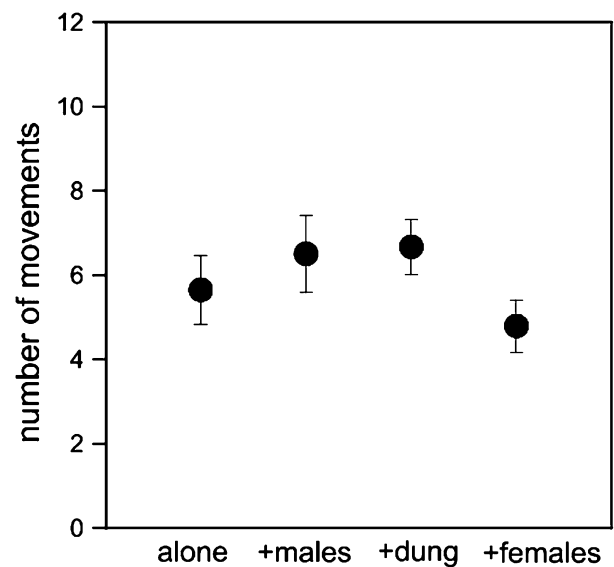


**Figure 2**
Mean mobility (number of movements ± SE) when males were alone, with other males without and with dung, or with females.

**Figure 3**
Male residual survival (starvation resistance) without food at 12 °C under different treatments (a) when testing young, virgin males: (1) 2–4 copulations, (2) 4 copulations + repose, (3) 2 copulations, repose, 2 copulations, (4) 1 copulation, (5) shaking, (6) male–male group, (7) alone without food (control 1), (8) from group container (control 2); or (b) when testing older, mass-held males: (9) alone without food, (10) 2 days alone with food, (11) alone without food then 2 days with food, (12) alone without food then 2 days in the mass container. $*P < 0.005$; $**P < 0.001$.
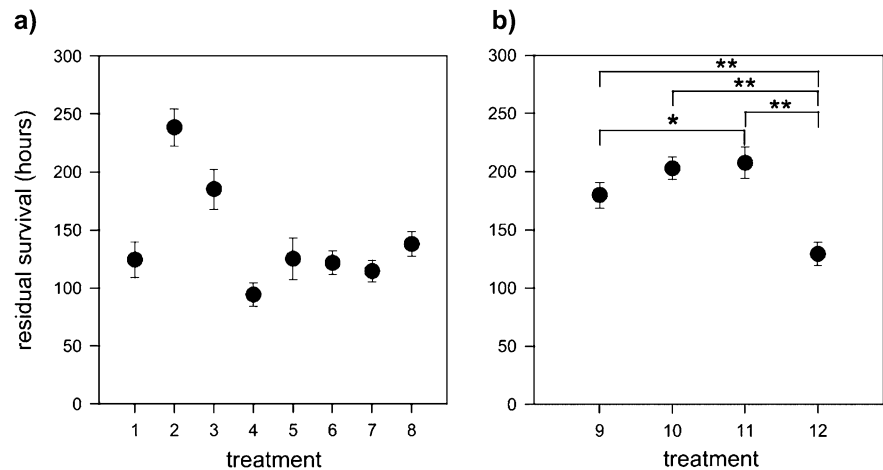


## DISCUSSION

Overall, we found no costs of mating for males. We found no indication that copulation, courtship, interactions with reluctant females, or short interactions with other males are energetically costly for males and ultimately translate into reduced survival when starved. Males were also not more likely to be predated than females. In contrast, body size influenced both predation and starvation risk, as smaller males tended to die sooner when starved and were preferred by the predator used here, the yellow dung fly *S. stercoraria*, which is very common around cow dung in north-central Europe.

As in Mühlhäuser and Blanckenhorn (2002), we found that in mixed-sex groups predation risk is not higher than in single-sex groups. This is unexpected, as mating is a conspicuous affair that should attract predators and at the same time distract prey. Additionally, our results suggest that the apparent higher predation risk of males found by Mühlhäuser and Blanckenhorn (2002) was probably due to their smaller size. Yellow dung flies are sit-and-wait predators that can catch prey ranging from *Drosophila melanogaster*, being much smaller than *S. cynipsea*, to the much larger *Musca domestica* (Blanckenhorn and Viele 1999). Thus, yellow dung flies should not be limited in their predatory ability within the size range of *Sepsis* flies and should actually prefer larger, energetically more profitable individuals (Stephens and Krebs 1986). In contrast, we found that yellow dung fly females prefer to catch smaller prey, independent of sex. Smaller individuals may be more mobile and hence more readily detected by predators. However, this hypothesis could be rejected here. If at all, male movement was more influenced by his motivation (to mate) rather than by his size. Sepsid flies are known to release a substance smelling like geraniums, which has been suggested to be a chemical defense against predation (Pont and Meier 2002). It could be that larger individuals release more of this substance and are therefore less likely to be eaten, at least by yellow dung flies. For example, birds seem to prey selectively on male monarch butterflies, probably because they contain fewer defensive chemicals (Brower and Calvert 1985). Based on one predator, our data suggest that larger *S. cynipsea* have a viability advantage. However, around a cow pat several other predators can be present. As each predator can impose a different selection pressure on body size and the 2 sexes, from the prey's perspective viability selection due to predation in the field may well have a different net result. Indeed, some amphibian predators prefer large *S. cynipsea* (Blanckenhorn WU, unpublished data).

Male *S. cynipsea* appear not to pay significant energetic costs for copulating or sexual activity, as virgin males did not survive for longer when starved than males copulating up to 4 times. Overall, being able to rest alone without other flies was the most important factor in extending a male's residual longevity (or starvation resistance: treatments 2, 3, and 9–11 in Figure 3). This is contrary to what was found for *Saltella sphondylii*, another Sepsid species (Martin and Hosken 2004), *Glossina morsitans morsitans* (Clutton-Brock and Langley 1997), *Caenorhabditis elegans* (Van Voorhies 1992), or *D. melanogaster* (Partridge and Farquhar 1981; Cordts and Partridge 1996), where males paid longevity costs for copulation per se and/or courtship. Our study therefore suggests that for *S. cynipsea* males, energetic costs of mating or enduring female shaking are minor in comparison to the stress of being exposed permanently to conspecifics. Mühlhäuser and Blanckenhorn (2002) showed previously that males held with other males had shorter residual life spans than males held with females or alone. Here, we showed that these costs are purely physiological, as males that were allowed to rest after having lived in all-male groups did not differ in residual longevity from singly held males. Males held in all-male groups tended to move slightly more, possibly leaving them less time to replenish sugar reserves. However, all this may well be a laboratory artifact, as males in the field can escape other males by leaving the cow pat, although they miss mating opportunities by doing so. Finally, rather than affecting survival, any costs of mating may become apparent only in other fitness components such as mating success, fecundity, or when males need to replenish their sperm reserves. Unfortunately, we do not know how often males copulate in the field and how much they deplete their sperm reserves. At least in the laboratory, some males are able to copulate successfully up to 5 times within 1 day (Teuschl and Blanckenhorn 2007).

Due to the relationship between surface and volume, small individuals are generally thought to be metabolically less efficient than larger individuals (Brown and West 2000). In addition to their known disadvantage in sexual selection (Ward 1983, Blanckenhorn et al. 1999, 2000, 2004), we have shown here that smaller males tend to starve faster, having either fewer reserves or using them less efficiently. Smaller flies were also more likely to be predated on by one prominent predator, despite not being more mobile than larger males. We conclude that any life-history costs paid by *S. cynipsea* males, particularly small males, mainly consist of energetic and predation costs in connection with mate search and/or scramble
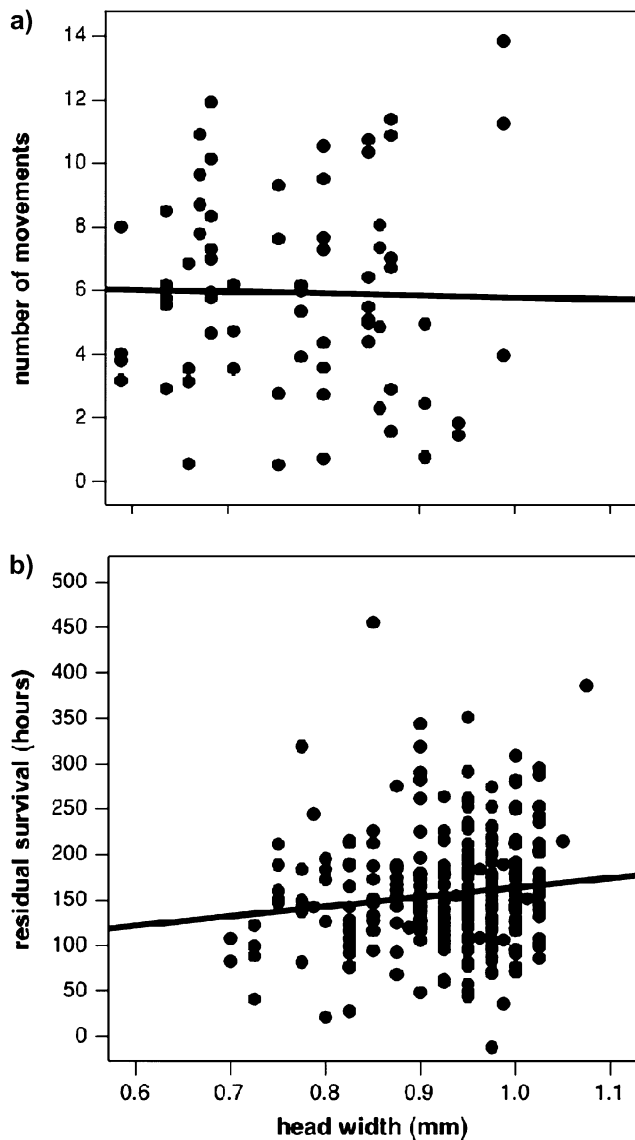
**Figure 4**
(a) Number of movements and (b) residual survival as a function of male body size (head with) with the effects of treatment controlled in both cases (cf. Figures 2 and 3).

competition with other males, though not necessarily in an immediate reproductive context. In comparison, mating itself and courtship appear energetically negligible. Overall, therefore, *S. cynipsea* seems to support the classic view that for males mating is cheap, whereas mate search and mate competition is more expensive. However, potential costs in terms of male fecundity or mating success remain to be investigated in this context.

**REFERENCES**

Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton University Press.

Arnqvist G. 1989. Multiple mating in a water strider: mutual benefits or intersexual conflict? Anim Behav. 38:749–756.

Arnqvist G, Nilsson T. 2000. The evolution of polyandry: multiple mating and female fitness in insects. Anim Behav. 60:145–164.

Bateman AJ. 1948. Intra-sexual selection in *Drosophila*. Heredity. 2:349–368.

Berger D, Walters R, Gotthard K. 2006. What keeps insects small? Size dependent predation on two species of butterfly larvae. Evol Ecol. 20:575–589.

Blanckenhorn WU, Hosken DJ, Martin OY, Reim C, Teuschl Y, Ward PI. 2002. The costs of copulating in the dung fly *Sepsis cynipsea*. Behav Ecol. 13:353–358.

Blanckenhorn WU, Kraushaar U, Teuschl Y, Reim C. 2004. Sexual selection on morphological and physiological traits and fluctuating asymmetry in the black scavenger fly *Sepsis cynipsea*. J Evol Biol. 17:629–641.

Blanckenhorn WU, Morf C, Mühlhäuser C, Reusch T. 1999. Spatio-temporal variation in selection on body size in the dung fly *Sepsis cynipsea*. J Evol Biol. 12:563–576.

Blanckenhorn WU, Mühlhäuser C, Morf C, Reusch T, Reuter M. 2000. Female choice, female reluctance to mate and sexual selection on body size in the dungfly *Sepsis cynipsea*. Ethology. 106: 577–593.

Blanckenhorn WU, Viele STN. 1999. Foraging in yellow dung flies: testing for a small male time budget advantage. Ecol Entomol. 24:1–6.

Blay S, Yuval B. 1997. Nutritional correlates of reproductive success of male Mediterranean fruit flies (Diptera: Tephritidae). Anim Behav. 54:59–66.

Brower LP, Calvert WH. 1985. Foraging dynamics of bird predators on overwintering monarch butterflies in Mexico. Evolution. 39: 852–868.

Brown JH, West GB. 2000. Scaling in biology. Oxford (United Kingdom): Oxford University Press.

Calow P. 1979. The cost of reproduction—a physiological approach. Biol Rev. 54:23–40.

Chapman T, Lidde LF, Kalb JM, Walfran MF, Partridge L. 1995. Cost of mating in *Drosophila melanogaster* female is mediated by male accessory gland products. Nature. 373:241–244.

Chapman T, Miyatake T, Smith HK, Partridge L. 1998. Interactions of mating, egg production and death rates in females of the Mediterranean fruit fly, *Ceratis capitata*. Proc Roy Soc Lond B. 265: 1879–1894.

Clutton-Brock T, Langley P. 1997. Persistent courtship reduces male and female longevity in captive tsetse flies *Glossina morsitans morsitans* Westwood (Diptera: Glossinidae). Behav Ecol. 8: 392–395.

Cordts R, Partridge L. 1996. Courtship reduces longevity of male *Drosophila melanogaster*. Anim Behav. 52:269–278.

Crudgington HS, Siva-Jothy MT. 2000. Genital damage, kicking and early death. Nature. 407:855–856.

Daley M. 1978. The cost of mating. Am Nat. 112:771–774.

Dunn DW, Crean CS, Wilson CL, Gilburn AS. 1999. Male choice, willingness to mate and body size in seaweed flies (Diptera: Coelopidae). Anim Behav. 57:847–853.

Fowler K, Partridge L. 1989. A cost of mating in female fruitflies. Nature. 338:760–761.

Gems D, Riddle DL. 1996. Longevity in *Caenorhabditis elegans* reduced by mating but not gamete production. Nature. 379:723–725.

Gibson RM, Langen TA. 1996. How do animals choose their mates? Trends Ecol Evol. 11:468–470.

Gwynne DT. 1989. Does copulation increase the risk of predation? Trends Ecol Evol. 4:54–56.

Gwynne DT. 1990. Testing parental investment and the control of sexual selection in katydids: the operational sex ratio. Am Nat. 136:474–484.

Hedrick AV, Dill LM. 1993. Mate choice by female crickets is influenced by predation risk. Anim Behav. 46:193–196.

Honek A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos. 66:483–492.

Jormalainen V, Merilaita S, Riihimäki J. 2001. Costs of intersexual conflict in the isopod *Idotea baltica*. J Evol Biol. 14:763–772.

Kotiaho J, Alatalo RV, Mappes J, Parri S, Rivero A. 1998. Male mating success and risk of predation in a wolf spider: a balance between sexual and natural selection? J Anim Ecol. 67:287–291.

LaMunyon CW, Eisner T. 1994. Spermatophore size as determinant of paternity in an arctiid moth (*Utetheisa ornatrix*). Proc Natl Acad Sci USA. 91:7081–7084.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool. 68:619–640.

Magnhagen C. 1991. Predation risk as a cost of reproduction. Trends Ecol Evol. 6:183–185.

Mand T, Tammaru T, Mappes J. 2007. Size-dependent predation risk in cryptic and conspicuous insects. Evol Ecol. 21:485–498.

Martin OY, Hosken DJ. 2004. Copulation reduces male but not female longevity in *Saltella sphondylii* (Diptera: Sepsidae). J Evol Biol. 17:357–362.

Mühlhäuser C, Blanckenhorn WU. 2002. The costs of avoiding matings in the dung fly *Sepsis cynipsea*. Behav Ecol. 13:359–365.

Pakku S, Kotiaho JS. 2005. Cost of reproduction in *Callosobruchus maculatus*: effects of mating on male longevity and the effect of male mating status on female longevity. J Insect Physiol. 51:1220–1226.

Parker GA. 1972. Reproductive behaviour of *Sepsis cynipsea* (L.) (Diptera - Sepsidae). II. The significance of the precopulatory passive phase and emigration. Behaviour. 41:242–250.

Partridge L, Farquhar M. 1981. Sexual activity reduces lifespan of male fruitflies. Nature. 294:580–582.

Pocklington R, Dill LM. 1995. Predation on female or males: who pays for bright male traits. Anim Behav. 49:1122–1124.

Pomiankowski A. 1987. The costs of choice in sexual selection. J Theor Biol. 128:195–218.

Pont AC, Meier R. 2002. The Sepsidae (Diptera) of Europe. Fauna Entomol Scand. 37:1–221.

Reynolds JD, Côté IM. 1995. Direct selection on mate choice: female redlip blennies pay more for better mates. Behav Ecol. 6:175–181.

Roff DA. 1992. The evolution of life histories, theory and analysis. London (United Kingdom): Chapman & Hall.

Rowe L. 1994. The cost of mating and mate choice in waterstriders. Anim Behav. 48:1049–1056.

Sheldon BC. 1993. Sexually transmitted disease in birds: occurrence and evolutionary significance. Phil Trans Roy Soc Lond B. 339:491–497.

Simmons LW. 1993. Quantification of role reversal in relative parental investment in a bush cricket. Nature. 358:61–63.

Simmons LW, Parker GA. 1992. Individual variation in sperm competition success of yellow dung flies, *Scatophaga stercoraria*. Evolution. 46:366–375.

Slagsvold T, Lifjeld JT, Stenmark G, Breiehagen T. 1988. On the cost of searching for a mate in female pied flycatchers *Ficedula hypoleuca*. Anim Behav. 36:433–442.

Stephens DW, Krebs JR. 1986. Foraging theory. Princeton (NJ): Princeton University Press.

Stutt AD, Siva-Jothy MT. 2001. Traumatic insemination and sexual conflict in the bed bug *Cimex lectualarius*. Proc Natl Acad Sci USA. 98:5683–5687.

Teuschl Y, Blanckenhorn WU. 2007. The reluctant fly: what makes *Sepsis cynipsea* females willing to copulate? Anim Behav. 73:85–97.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man. Chicago (IL): Aldine. p. 136–179.

Vahed K. 1998. The function of the nuptial feeding in insects: a review of empirical studies. Biol Rev. 73:43–78.

Van Voorhies WA. 1992. Production of sperm reduces nematode lifespan. Nature. 360:456–458.

Ward PI. 1983. The effects of size on the mating behaviour of the dung fly *Sepsis cynipsea*. Behav Ecol Sociobiol. 13:75–80.

Ward PI, Hemmi J, Röösli T. 1992. Sexual conflict in the dung fly *Sepsis cynipsea*. Funct Ecol. 6:649–653.

Watson PJ, Arnqvist G, Stallmann RR. 1998. Sexual conflict and the energetic costs of mating and mate choice in water striders. Am Nat. 151:46–58.

Wellborn GA. 1994. Size-biased predation and prey life histories: a comparative study of freshwater amphipod populations. Ecology. 75:2104–2117.

Yanagi S, Miyatake T. 2003. Costs of mating and egg production in female *Callosobruchus chinensis*. J Insect Physiol. 49:823–827.

Zuk M, Kolluru GR. 1998. Exploitation of sexual signals by predators and parasitoids. Quart Rev Biol. 73:415–438.