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Swarming and mating behavior of a mayfly *Baetis bicaudatus* suggest stabilizing selection for male body size

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Abstract Large size often confers a fitness advantage to female insects because fecundity increases with body size. However, the fitness benefits of large size for male insects are less clear. We investigated the mating behavior of the mayfly *Baetis bicaudatus* to determine whether the probability of male mating success increased with body size. Males formed mating aggregations (swarms) ranging from a few to hundreds of individuals, 1–4 m above the ground for about 1.5–2 h in the early morning. Females that flew near swarms were grabbed by males, pairs dropped to the vegetation where they mated and then flew off individually. Some marked males returned to swarms 1, 2 or 3 days after marking. Larger males swarmed near spruce trees at the edges of meadows, but the probability of copulating was not a function of male body size (no large male advantage). Furthermore, the potential fitness advantage of mating with larger, more fecund females was not greater for large males (no size-assortative mating). However, the sizes of copulating males were significantly less variable than those of non-mating males collected at random in swarms. Intermediate male size may be optimal during mating because of trade-offs between flight agility and longevity or competitive ability. Results of this study are consistent with the hypotheses that there is stabilizing selection on adult male body size during mating, and that male body size in this species may be influenced more by selection pressures acting on larvae than on adults.

Keywords Body size · Large male advantage · Mayfly swarms · Size-assortative mating · Stabilizing selection

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Introduction

It is often assumed that larger individuals of a species have a fitness advantage over smaller individuals, especially among the insects (Wickman and Karlsson 1989). The rationale behind this assumption is that larger individuals may be better competitors for food (Wilson 1975) or mates (Alcock 1998), or have greater survivorship or longevity (e.g., Sokolovska et al. 2000). Furthermore, selection for higher fecundity favors larger females (Honek 1993); but the reproductive advantages of being a large male are not as clear. Males and females are often subjected to different selection pressures, which can result in sexual size dimorphism (Fairbairn and Preziosi 1994). While natural selection favors large females that produce more eggs, sexual selection in the form of male–male competition or female choice can result in larger body size in males (e.g., Fairbairn 1997).

Large males have a mating advantage in many species of arthropods. Large males of some arthropod species increase their potential relative fitness by mating with larger, more fecund females (size-assortative mating) (Crespi 1989; Arnqvist et al. 1996; Rowe and Arnqvist 1996). In some species of insects, larger males have a higher probability of obtaining mates (Flecker et al. 1988; Savalli and Fox 1998), especially males that use large size to attract females to their territories, or to fend off intruding males (Alcock 1990; Mathis 1991; Sokolovska et al. 2000). Large size can also benefit males that must

overcome female rejection or aggression (Weigensberg and Fairbairn 1999), or increase the probability of paternity by preventing intruder males from take-overs during prolonged copulations (Naylor and Adams 1987; Alcock 1994). Large size may improve mating success of males with elaborate courtship behaviors, making these behaviors more conspicuous or attractive to females (Smith 1979). Finally, for males that swarm, large size may be associated with higher energy reserves enabling them to maintain flight for longer periods (Petersson 1987; Sartori et al. 1992).

In many organisms there are conflicting selection pressures operating on body size of both males and females (Schluter et al. 1991). Potential costs of large body size in animals include: higher mortality rates due to longer juvenile development times, increased energy demands, increased conspicuousness to predators or parasites, and increased heat stress (Blankenhorn 2000). Furthermore, larger individuals of a species may have a mating disadvantage if attaining large size is associated with late reproduction, or increased energy requirements. Other trade-offs may cause selection against large size only in males. For example, large male size may increase the burden for females of species that carry males during long post-copulatory periods, resulting in female-biased sexual size dimorphism (Taylor et al. 1998). Furthermore, if flight is a requirement for successful mating (as in mayflies), large size associated with decreased agility could reduce male fitness, as has been shown for other insects (McLachlan and Allen 1987; Marden 1987, 1989b; Neems et al. 1990). Therefore, conflicting selection pressures especially on male size may result in no apparent large male advantage, or stabilizing selection for some optimal intermediate size with maximum lifetime fitness (Thompson 1989; Schluter et al. 1991; Neems et al. 1998; Preziosi and Fairbairn 2000; Stoks 2000).

Mayflies typically have very short-lived adult stages, and are the only extant order of insects with two winged stages (the subimago and imago) (Brittain 1982; Edmunds and McCafferty 1988). Mayfly adults (of all species) do not feed, as mouthparts atrophy during metamorphosis from the last larval instar to the subimago stage. Thus, females produce all their eggs as larvae, and fecundity is strongly correlated with adult female size (see citations in Peckarsky et al. 1993, 2001; McPeek and Peckarsky 1998). Male imagoes form aerial mating aggregations (swarms), presumably to attract females. Female imagoes typically fly into these swarms, copulate in the air, and then fly to oviposit in the aquatic habitat. However, some females mate as subimagoes (Spieth 1940; Berner and Pescador1988; Edmunds and McCafferty 1988), and others mate on the ground or on vegetation (Spieth 1940). The longest-lived mayfly adults reported are females of species that are ovoviparous, mate as subimagoes, and then incubate their eggs for up to 2 weeks (e.g., *Callibaetis*, Edmunds et al. 1976; Caudill, unpublished data). More typically, adult males and females live for 1–4 days (Edmunds et al. 1976; Brittain 1982). Male (e.g. *Epeorus*: Flecker et al. 1988; Allan and Flecker 1989) and female mayflies (e.g., *Tricorythodes*: Newell and Minshall 1978; *Callibaetis*: Caudill, unpublished data) have been observed returning to swarms on subsequent days, but multiple paternity remains to be established (Harker 1992).

For male mayflies, the costs associated with attaining a large adult size may be substantial. Individual larvae must either grow faster or spend more time in the aquatic habitat to reach larger adult sizes, which would increase their exposure to predation. Many predators on larval mayflies are also size-selective for larger prey (Allan 1981). We have observed that *Baetis bicaudatus* Dodds (Ephemeroptera: Baetidae) larvae of both sexes developing in trout streams sacrifice potential large size by maturing at smaller sizes, presumably to reduce their exposure to predatory brook trout (Peckarsky et al. 2001). While the costs of reduced size are clear for females, the purpose of this study was to observe the mating behavior of *B. bicaudatus* to investigate whether smaller male size reduces male fitness. A large male advantage in mating swarms or size-assortative mating could result in conflicting larval and adult selection pressures on males, as is the case for females. Alternatively, there could be selection for smaller adult male size or no loss of fitness if male size does not affect mating success. To evaluate these hypotheses we conducted observations of adults in 1992, 1996 and 1999 to determine the relationship between male size and longevity, swarming and mating success, and also tested whether large males attained a fitness advantage by size-assortative mating with larger females.

Methods

Study sites and local population attributes

Baetis bicaudatus larvae are present in streams of the East River catchment near the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado, USA, ranging from the highest elevation headwater streams to larger streams at 2,900 m elevation at the RMBL town site (Peckarsky et al. 2000). The flight period of this univoltine species varies annually depending on the hydrologic regime; but swarms usually extend from late June to early August.

In 1992 and 1996 we studied swarms of *B. bicaudatus* in an east-facing meadow adjacent to Lower Benthette Brook (2,910 m), a small tributary of the East River draining Gothic Mountain west of RMBL (Peckarsky et al. 2000). This meadow was ~10×20 m with the long axis running east-west. The south edge was bordered by 5–7 m high spruces and the north border was a steep, dry slope leading up to a larger meadow. Patches of riparian willows and a few spruces were scattered along the stream. In 1999 we studied *B. bicaudatus* swarms in a larger (~20×30 m), west-facing meadow at ~3,200 m elevation, also steep, with the long axis running east-west, and bordered by large spruce trees and scattered shrubs. Unlike the lower elevation meadow, this site was relatively distant from the nearest stream (0.5 km from Virginia Creek), another small tributary of the East River draining Virginia Basin east of RMBL (see maps in Peckarsky et al. 2000).

Qualitative behavioral observations

In July 1992 at the lower elevation meadow, we recorded the behavior of four different *Baetis* swarms on three different dates

from 0830–1030 hours Mountain Daylight Time (MTD) beginning ~1.5 h after sunrise. We similarly observed 18 swarms of *Baetis* in July – early August 1996 at this same location, for a total of 22 h of observation. The purpose of these observations was to describe the general characteristics of *B. bicaudatus* swarming behavior, such as size and location of swarms, timing of swarming behavior, nature of male and female flight patterns, and coupling and copulation.

Quantitative observations

Spatial segregation by male size

On 26 July 1996 at the lower-elevation site we took samples of swarming males to test for size differences between males flying under different optical conditions and over different swarm markers (conspicuous objects that could be used as visual cues, cf. Sullivan 1981). We compared the sizes of males flying in loose swarms in the shadow of spruce trees bordering the meadow to that of males flying in direct sunlight in tight swarms above individual willows in the middle of the meadow. The two sampling locations were separated by <10 m. We measured male mesonotum length to the nearest 0.02 mm, using an eyepiece micrometer on a Wild dissecting microscope, and tested for differences in male size between locations with a one-way ANOVA. The purpose of these observations was to determine whether large and small males segregated spatially in a way that could affect mating success. Swarms were comprised exclusively of males; no females were collected in these samples.

Male longevity

A mark-recapture study was performed in 1996 at the lower-elevation site to determine whether males returned to swarms on subsequent days (as a conservative estimate of longevity). Males were marked and recaptured during two 5-day periods (22–26 July and 5–9 August). Males were captured with a sweep net while swarming and marked on one wing with a Sharpie Brand permanent marker, and then released. Different colors were used on different days to estimate the number of days that marked males swarmed. Marking did not appear to affect male behavior, because marked males were frequently observed in swarms immediately after being handled. Recaptured males were immediately released during the first 5-day period, but were collected for size measurements (mesonotum length) during the second 5-day period. Since we did not estimate marking mortality, and the age of males first captured was unknown, these data provide a conservative estimate of the minimum longevity.

Large-male advantage and size assortative mating

On 26 and 28 July 1999 from 0945–1100 hours MDT, we used a sweep net to collect copulating pairs of *B. bicaudatus* at the high-elevation location. For each individual collected, we measured the length of the entire wing to the nearest 0.02 mm, using an eyepiece micrometer on a Wild dissecting microscope, and dry weight (mg) on a Cahn microbalance, after drying individuals for 24 h. We compared the sizes of males in copula to sizes of males collected at random from swarms during those same time periods (as in Flecker et al. 1988). We measured wing length and dry weight of 34 copulating pairs (males and females) collected over the 2 days, and of 7 samples ranging from 16 to 37 males collected randomly from swarms at approximately half-hour intervals each day. Since male size did not change during the swarming period on either date or between sampling dates (nested ANOVA: $F_{1,5}$=0.097, P=0.77 and $F_{5,165}$=0.448, P=0.82, respectively) all males were combined across the two sampling dates for analysis (total of 173 swarming males). We used multiple binary logistic regression (Hosmer and Lemeshow 1989) to test for associations between mating status and male mass, wing length, and the ratio of mass/wing length. We assumed that male mayflies with larger relative muscle mass could potentially swarm longer thereby increasing the probability of female encounters. Thus, larger mass/wing length is an indirect measure of flight muscle ratio, which has been associated with successful mating in other species of insects (e.g., Marden 1989a). We used Pearson correlation analysis to look for associations between sizes of males and females in copula (size-assortative mating).

Finally, we tested whether the observed patterns of sizes of mating and non-mating males were consistent with the hypothesis that stabilizing selection results in higher probability of mating for males of intermediate size. We compared the coefficients of variation (CV) of the size distributions for mating and non-mating males to test whether the size of successful males was less variable than that of the population of swarming males (as in Rutowski 1985). Since sample sizes of mating (34) and non-mating (173) males were unequal, we generated a 95% confidence interval (CI) for the CV of non-mating males by bootstrapping with replacement using 1,000 replicate subsamples of 30 non-mating individuals (in Systat v 7.0, SPSS, Chicago, Ill.). We considered the CVs of the mating and non-mating males to be significantly different if the CV for mating males fell outside the 95% confidence interval of non-mating males generated by the bootstrap analysis.

Results

Qualitative behavioral observations

Timing and size of swarms

Baetis bicaudatus males swarmed from late July to early August at the lower-elevation site in both 1992 and 1996. Swarming lasted for 1.5–2 h each morning starting at approximately 0800 hours at the beginning of the season and progressively later through the flight period (0830–0845 hours MDT during the first weeks of August). No swarming was observed after 1015 hours on any date in either year. At the low elevation meadow, ~100 males swarmed in a loose aggregate containing several distinct sub-swarms ranging from 15 to 20 individuals. Size of these sub-swarms gradually decreased to zero during the swarm period each day rather than dispersing all at once, and individuals occasionally switched from one sub-swarm to another within the meadow. We had never observed *B. bicaudatus* swarming along the main stem of the East River until 1999 when large swarms were observed in July above willows in the RMBL town site. Swarms observed at the higher-elevation location in 1999 were also very large, containing hundreds of individuals with no distinct sub-swarms. Furthermore, the onset of swarming at this higher elevation site (~3,200 m) was an hour later, and continued about an hour after swarming ceased at ~2,900 m.

Male flight in swarms

Males swarmed at heights of 1–4 m above the ground, frequently over swarm markers such as a tall shrubs or willows. At the lower-elevation site, swarms in the open meadow were 0.5–2 m above willows and the largest swarms were 1.0–1.5 m in diameter. Individual males exhibited a characteristic vertical nuptial dance typical of

most species of mayflies (type "A" of Brodskiy 1973; Fisher 1984; Allan and Flecker 1989), ascending with their bodies pitched approximately 70° from horizontal and flying slightly backwards. At the top of their flight, their bodies pitched back to horizontal while they flew forward slightly. Males then descended passively at a slower rate with wings and cerci extended clearly providing drag. The body axis was parallel to the ground during the passive descent. The net flight path viewed laterally was a tight figure 8 with the larger loop at the top and amplitude of 0.5–1.0 m. Through most of the swarm period each day males displayed this smooth flight behavior, but occasionally swarms became more "frantic" and the flight paths of males were more chaotic.

Most males swarmed in the sunshine; but occasionally males swarmed in the shade along the spruce margin at the south edge of the lower-elevation meadow. While the flight patterns of individual males in the spruce shadows were similar to the those of males in the sun, males in the shadow flew higher off the ground (1.5–3.0 m), and were relatively dispersed along the spruce margin compared to the strongly aggregated males in the sun. Males at the higher-elevation location swarmed in the sunshine, and extended the amplitude of their flight paths up to 4.0 m. Males at both locations could be seen interacting, chasing each other and grappling frequently. Swarming males were also observed chasing other flying insects such as stoneflies and dipterans.

Female flight

Few females were observed in flight at the lower-elevation site, probably because they were resting in vegetation below swarms, as has been reported for other species of mayflies (Harker 1992). Flying females were conspicuous because their flight was slow compared to that of males, and their body color was lighter and more yellow. Females flew in a horizontal, circling pattern 1.0–1.5 m above the ground with their bodies pitched nearly vertical (~80–90° above horizontal). Females were rarely observed flying into either the smooth or "frantic" swarms at the lower-elevation location, but more commonly observed flying through the larger, higher-elevation swarms.

Coupling and copulation

Females flying near swarms at both locations were approached and grabbed by males. On one occasion in 1996, two different males attempted to grab, but missed, the same female during a 10-s period, and she was grabbed and mated by a third male approximately 5 s later. Occasionally, a mating pair hovered for up to 5 s with the female motionless and the male carrying the weight of the pair. More typically, pairs descended immediately to the vegetation and remained coupled in the typical posterior to posterior position for up to 2 min. Copulation ended when either the male or the female flew off followed shortly by the other.

Male–male pairs

Of 5 pairs collected in 1996, 1 was male–male, 3 of 37 total pairs collected in 1999 were male–male, and in 1999 1 triplet was collected comprised of one female and two males. Whether these represented brief "mistakes" by males or if sperm transfer was attempted by one or the other male is unknown. The male–male pairs looked superficially similar to heterosexual pairs in flight, but remained coupled long enough to be recognized and collected.

Quantitative observations

Spatial segregation by male size

In 1996 at the lower elevation site males swarming in the shadows along the spruce margin were significantly larger (mean±SE mesonotum length=1.763±0.016 mm) than males swarming in the open meadow in the sunshine (mean±SE mesonotum length=1.666±0.015 mm) (one-way ANOVA, F=18.279, n=60, P<0.001). These data indicate that there was some temporal and spatial segregation of large and small males swarming at the lower-elevation site in 1992 and 1996.

Male longevity

Forty-seven of 812 marked male *B. bicaudatus* from approximately 8 swarms were recaptured one or more days after being marked at the lower-elevation site in 1996. All were recaptured at the study site, except one marked male that was found in a swarm 100 m downstream of the study site 1 day after being marked. Most (40) were recaptured in swarms 1 day after marking, but five males were recaptured 2 days after marking and 2 males were recaptured 3 days after being marked. These data demonstrate that some males swarmed for two consecutive days, and that a few males lived for as many as 4 days (marked on day 0 and recaptured on day 3). Since the age of the marked males was unknown, these data provide a conservative estimate of male longevity. Male size (mean mesonotum length) of males recaptured on day 2 (1.515 mm) was smaller than those recaptured on day 1 (1.635 mm), suggesting that there was no longevity advantage for large males.

Large-male advantage and size assortative mating

We found no evidence that large males had a mating advantage in swarms at the higher-elevation site in 1999.

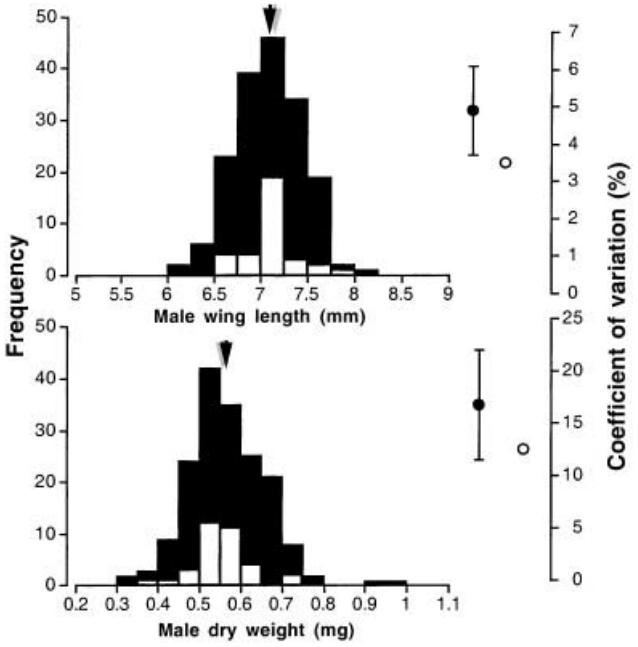


Fig. 1 Size-frequency distributions (wing length – *upper*, dry weight – *lower*) of male *Baetis bicaudatus* collected at random from swarms (*black bars*: *n*=173) or copulating with females (*open bars*: *n*=34) on 26 and 28 July 1999 at the higher elevation meadow near Virginia Basin. *Black arrows* indicate the mean size of males in the swarms, and *grey arrows* show the mean size of copulating males. On the *right vertical axis* we have plotted the mean coefficient of variation (CV) of the size of copulating males (*open circles*), and mean±95% confidence intervals of the CV of size of males collected from swarms (*black circles* and *error bars*)

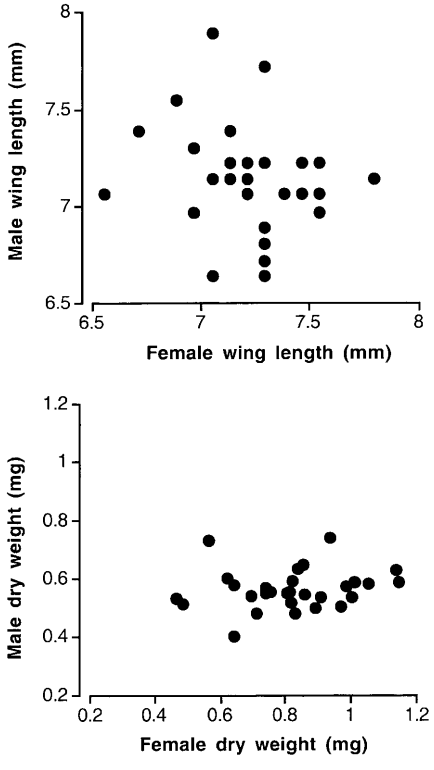


Fig. 2 Relationship between size (wing length – *upper*, dry weight – *lower*) of female and male *Baetis bicaudatus* in copula

Mating males could not be predicted from their dry mass, wing length, or mass to wing length ratio (multiple logistic regression model, chi-square=2.118, 3 *df*, P=0.548, r^2=0.012). Thus, copulating males were neither larger nor smaller than non-mating males collected at random from swarms (Fig. 1). Furthermore, there was no correlation between the sizes of males and females in copulating pairs (Fig. 2, r=0.17 and r=–0.20 for dry weight and wing length, respectively, P>0.05, n=30).

However, the bootstrap analysis of variability in the size of mating versus non-mating males indicates that the size of copulating males was less variable than the sizes of males in the swarming population as a whole (Fig. 1). Wing length was significantly less variable in mated males (CV=3.5%) than non-mated males (95% CI for non-mated males=3.7–6.1%). The same pattern was observed for body mass; however the observed value for mated males (CV=12.6%) fell within the lower limit of the 95% CI of non-mating males (11.5–22%).

Discussion

Our data provide no evidence of a large male advantage for *Baetis bicaudatus*, since mating success did not increase with male size. Similarly, the potential fitness advantage of mating with larger, more fecund females was not greater for large males (no size-assortative mating). These results differ from the only other published studies that directly tested for a large male advantage in mayflies. Flecker et al. (1988) showed that copulating mayfly males of *Epeorus longimanus* (Heptageniidae) were significantly larger than males collected at random from swarms on three different dates at another location near RMBL. Harker (1992) found that larger males of several species of mayflies had discharged a greater proportion of their sperm, and suggested that this observation provided indirect evidence for a higher mating success for large males. Instead, our data are consistent with the hypothesis that stabilizing selection may favor intermediate sized males, and select against the largest and smallest males in the population because of trade-offs between large and small size.

There is no general pattern for mating success versus male size in insects, because the traits that improve male mating success depend on the mating system of each species. However, intermediate-sized males of other species of insects have been shown to have greater lifetime fitness resulting from trade-offs between being large and being small. For example, large male damselflies lived longer, but had lower mating rates per day conferring lower mating success for males at both extremes of the size spectrum (Fincke 1982; Banks and Thompson 1985; Stoks 2000). Small male chironomids, which also do not feed as adults, have been shown to be more agile fliers (McLachlan 1986), but can not sustain flight as long as larger males (Neems et al. 1990). While small males captured more females within swarms, larger males lived longer and remained in swarms longer, which resulted in

a trade-off whereby intermediate-sized males had the greatest lifetime fitness (Neems et al 1998).

Are there trade-offs associated with male size in *B. bicaudatus?* This question needs to be viewed in the context of the different selection pressures acting on larvae and adults. Interestingly, the maximum body sizes attained by mature larvae of males and females covary among different natural streams (Peckarsky et al. 2001), suggesting that factors affecting growth and development of larval stages of males and females are similar. Larger *Baetis* larvae of both sexes are more vulnerable to predation by trout (Allan 1978, 1981) and by large predatory stoneflies (Allan et al. 1987; Allan and Flecker 1989), which should increase survival of small *Baetis* larvae. Thus, while female *Baetis* should experience conflicting selection pressure to attain a larger adult body size due to the fecundity advantage, without strong selection to be a large adult, selection pressure to reduce larval mortality from predation should predominate in male *Baetis*. In contrast, larvae of *E. longimanus*, the mayflies that have a large male advantage in swarms, are rare in the diets of trout (Allan 1981) and stoneflies (Peckarsky 1985). Therefore, males of *Epeorus* would be under less selection pressure to emerge at smaller body size than males of *Baetis*.

Given this size-dependent survival for *Baetis* larvae there should be net directional selection on males to emerge at a smaller size. However, greater mating success for intermediate-sized males suggests that balancing selection favors adult males of average size. We suspect that this pattern results from trade-offs between being a large or small adult male. The return of males to swarms on subsequent days and rarity of females flying near swarms suggest that access to females, which only mate once, may be limited in this species. Thus, larger males may benefit during scramble competition for limited females, as has been demonstrated for other species of insects (e.g., *Epeorus*: Flecker et al 1988; territorial dragonflies: Sokolovska et al 2000; weevils: Johnson 1982; soldier flies: Alcock 1990; earwigs: Forslund 2000; see review in Thornhill and Alcock 1983). However, smaller males may be more agile under scramble competition in swarms (McLachlan and Allen 1987), while larger males may have greater energy stores, enabling them to sustain flight longer (Marden 1989b). These sorts of trade-offs may be responsible for the observed fitness advantage of intermediate-sized adult males, as has been shown in chironomids (Neems et al. 1998).

Comparisons between the mating systems of *Baetis* and *Epeorus* may provide further insights into the selection pressures resulting in higher mating success for intermediate-sized *Baetis* males. First, while *Epeorus* copulates in flight, *Baetis* typically copulates resting on vegetation, which does not necessitate achieving large size to improve the capability of bearing the load of the females (e.g., Marden 1989a). Second, *Epeorus* and *Baetis* exhibit opposite patterns of sexual size dimorphism, suggesting that selection on body size differs between these two species. These patterns of sexual size dimorphism can be used to make inferences about selection pressures on male size in the adult stages, because directional selection for larger, more fecund females operates in both species. Notably, male *Epeorus* are larger than females (Flecker et al. 1988, Table 1; an example of reversed sexual size dimorphism), suggesting the presence of strong sexual selection on male body size (Fairbairn 1997), especially considering that female *Epeorus* larvae are less vulnerable to predation than *Baetis*. The converse is true for *Baetis* (females larger than males, Peckarsky et al. 1993, 2001), suggesting that males of this species are under less intense selection to be large (as in chironomids, McLachlan 1986).

We originally suspected that the spatial segregation of large and small males observed in 1996 swarms could be related to access to females or a light regime affecting detection of females (Savolainen 1978; Branstrom 2002). If females rest in the spruces while molting into imagoes and then fly toward male swarms, the best place for males to swarm would be at the spruce margin, similar to the spatial advantage obtained by lekking march flies (Thornhill and Alcock 1983) or large morph males of burrowing bees (Alcock 1997). However, Flecker et al. (1988) found no advantage to *Epeorus* males on the periphery of swarms, and we found no large male advantage in *Baetis*. Possibly, larger males may swarm in the shadows to control their body temperatures (Heinrich 1993), or to conserve energy.

It is possible that the two measures of size that we used in the 1999 study were not relevant indicators of male performance. Wing length did not correlate strongly with body mass in *B. bicaudatus* (r^2=45%), and male body mass was more variable than wing length (Fig. 1). Part of this variability may arise because males within each size class were of different ages, which could contribute to variation of fat stores (e.g., Petersson 1989; Sartori et al. 1992; Yuval et al. 1994). It would be useful to determine whether variation in the age of *Baetis* males independent of body size affects male mating success, as has been demonstrated in other species of insects (Fincke 1982; Kemp 2000).

In conclusion, *B. bicaudatus* provides an example of an insect species in which large size does not appear to confer an advantage in mating success for males. Instead, our data provide evidence that stabilizing selection favors an optimal intermediate size for males, resulting in lower mating success for males at both extremes of the size spectrum.

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