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Can minor males of Dawson's burrowing bee, *Amegilla dawsoni* (Hymenoptera: Anthophorini) compensate for reduced access to virgin females through sperm competition?

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Dawson's burrowing bees (*Amegilla dawsoni*) exhibit a conditional mating strategy with two alternative tactics. Large (major) males exclusively patrol emergence sites in search of about-to-emerge females, whereas small (minor) males usually search the periphery of emergence sites for females that escape patrollers. About 80% of the male population are minors, despite the fact that patrolling emergence sites is apparently the more profitable mating tactic. We tested the hypothesis that minor males gain fitness by mating with nonvirgin females and engaging in sperm competition with rival ejaculates. If the sperm competition hypothesis applied, it would help explain why nesting females produce so many minor sons. Contrary to this hypothesis, however, we found that minor males do not exhibit traits frequently associated with sperm competition. Minor and major males did not differ in testis mass after controlling for body size. Neither did they differ significantly in the duration or pattern of copulation nor in the volume of ejaculate transferred. In addition, and also contrary to the sperm competition hypothesis, females apparently mated only once. Loss of female sexual receptivity occurred quickly after the onset of copulation, and nesting females appeared completely unreceptive. Thus, all aspects of the bee's mating system strongly indicate that sperm competition does not occur in Dawson's burrowing bee, so that minors cannot compensate even partially via sperm competition for their mating disadvantage with virgin females. *Key words:* alternative mating tactics, *Amegilla dawsoni,* bees, sperm competition. *[Behav Ecol 11:319–325 (2000)]*

Studies of animal mating systems have revealed considerable intraspecific variability in mate-securing tactics (Andersson, 1994; Thornhill and Alcock, 1983). In many cases males have various morphological and/or life-history traits that facilitate their alternative mating behavior. Although the evolutionary maintenance of alternative phenotypes has been the subject of intense theoretical investigation, few empirical studies have examined fitness parameters associated with alternative tactics in natural populations (Gross, 1996).

The mating system of Dawson's burrowing bee, *Amegilla dawsoni,* is characterized by a conditional mating strategy with two alternative tactics. Two size classes of male exist, small minors and large majors, with male size dependent on the amount of brood provisions received from their mother (Alcock, 1997a, 1999; Houston, 1991). The two size classes of males adopt alternative mating tactics (Alcock, 1997a). Males emerge earlier than females (Alcock, 1997b), and major males patrol the emergence site for about-to-emerge females. Competition for access to emerging females is intense, and larger males have a competitive advantage over smaller males (Alcock, 1996c). Minor males thus search the peripheral zone of emergence sites for females that escape patrolling majors or search at flower patches where females forage (Alcock, 1997a). Patrolling emergence sites is the more profitable tactic, with nearly 90% of all virgin females mating with patrollers immediately upon their emergence (Alcock, 1996c). Although minor males patrol emergence areas when the intensity of competition is low, usually they are forced into the low-payoff tactic, yet they represent 66–80% of the male population (Alcock, 1997a).

Field studies of this bee have attempted to discover how the production of such high frequencies of minor males by nesting females can be maintained (Alcock, 1996c). First, male size dimorphism cannot represent an incidental by-product of environmental constraints because dimorphisms persist across generations, vary little between populations, and are specific to male offspring. Second, male dimorphism does not arise because of the occurrence of two classes of female that exhibit two different condition-dependent provisioning tactics, because putative siblings can be of either major or minor phenotype. A third hypothesis is that individual females produce minors that on average return the same net fitness benefit as major male offspring; although minors are constrained to adopt a much less profitable tactic, they are about half as costly to produce as majors, based on the quantity of provisions they require, and survive on average 22% longer at the emergence area (Alcock, 1996a). Nonetheless, because minors obtain less than half the observed copulations while constituting substantially more than half the male population, a balance in the cost:benefit ratio for the two morphs seems unlikely (Alcock, 1996b). However, to date payoffs have been estimated only on matings observed at emergence sites. Multiple mating by females and subsequent sperm competition from minor males could alter the fitness payoffs to nesting females from producing minor sons and thereby at least partially compensate for the poor mating success of minors at emergence sites (Alcock, 1996b).

If sperm competition is an important aspect of the mating

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system of Dawson's burrowing bee, a number of testable predictions emerge. First, recent game theoretical models of sperm competition predict that males adopting alternative, less profitable mating tactics should invest more heavily in traits that promote success in sperm competition (Parker, 1990). Minor males searching away from emergence areas will always be subject to sperm competition given the high probability that a female will have already mated at the emergence site. In contrast, major males should be subject to low probability of sperm competition, dependent on the encounter rate of females with minors away from emergence sites. With this expected asymmetry in sperm competition risk, Parker's models predict that minor males should compensate for low mating probability by allocating more resources to sperm production, ejaculating greater volumes of sperm during copulation, and/or spending longer in copulatory activities than major males (de Fraipont et al., 1993; Gage et al., 1995; Simmons et al., 1999; Taborsky, 1998).

Second, some females should exhibit a tendency to mate with more than one male. In at least one anthophorine, the solitary bee *Centris pallida,* some females will mate a second time if they have received incomplete copulatory and postcopulatory stimulation (Alcock and Buchmann, 1985). We show here that copulatory and postcopulatory courtship also occur in *A. dawsoni,* raising the possibility that those females that do not receive sufficient stimulation from their first mate may copulate a second time, possibly with a minor male away from the emergence site.

We tested the predictions concerning male investment in ejaculate production and male and female copulatory behavior to assess the general significance of sperm competition as a factor in maintaining the high frequency of minor males in populations of Dawson's burrowing bee.

METHODS

The study was conducted during the 1997 reproductive season at an emergence site 10 km north of Carnarvon, Western Australia (see Alcock, 1996c). All observations were made between 1030 and 1600 h, the peak period of bee activity. We collected males as they patrolled the emergence site searching for about-to-emerge females or from the periphery of the emergence site. When patrolling males alighted on the ground by an emergence tunnel, a small vial was placed over the entrance to collect the emerging female. We also collected nesting females as they returned to their burrows from foraging trips.

Variation in testis mass

We captured patrolling and searching males and placed them immediately into a refrigerator in our field vehicle. Males were later weighed and the width of their head capsule determined (head capsule width is the standard measure of body size used for bees; Stubblefield and Seger, 1994)before being frozen in liquid nitrogen for transportation back to the laboratory. Testes were later dissected and weighed to the nearest 0.01 mg.

Variation in male mating behavior

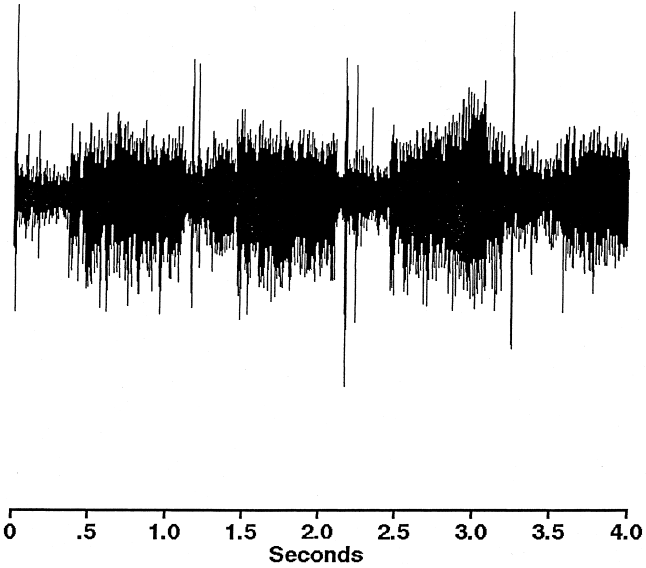

Figure 1
Acoustic interactions between male and female *Amegilla dawsoni* during copulation. The oscillogram shows a sequence of zips recorded early in phase 2 of copulation when zips occur at about 1/s. Note how the female's response buzz increases in amplitude about 0.3 s after the male's zip (the first zip in this sequence occurs at 0 s) and declines again immediately before the male's next zip.

We placed newly emerged females into an insect net and isolated them in a small pouch approximately 30 cm^3 by gathering and twisting the net beneath the female. A patrolling male was captured and placed immediately into the pouch with the female. Males typically pounced on the female as soon as they came into contact, and their copulatory behavior was then recorded. The bee's copulatory behavior is characterized by three distinct phases. In phase 1, the male positions himself onto the female's back and flicks his wings forward a number of times. Phase 2 begins immediately upon intromission, during which the male produces a continuous series of rapid, shallow body thrusts that are accompanied by an audible "zip" to which the female responds with a buzz (Figure 1). During phase 3, the male disengages his genitalia but continues to "zip". Zips are interspersed with deeper backward movements, during which the male probes the female's external genitalia with his own genitalia and flutters his wings. We recorded (1) the number of flicks during phase 1; (2) the number of zips within each minute of copulation during phase 2; and (3) the number of zips and the number of flutters within each minute of phase 3. All animals were placed in the refrigerator and weights and head capsule widths determined before freezing the bees in liquid nitrogen.

To determine whether males behaved normally in the net, we recorded copulations that were initiated by patrolling males at the emergence site. Males mount females as they emerge and ride on their backs across the open ground of the emergence site to vegetation at its periphery. We followed six pairs and recorded their copulatory behavior in the peripheral vegetation.

Variation in sperm transfer

We monitored sperm transfer by interrupting copulations after varying periods: 1 zip (about 1s), 5 zips (about 5 s), 15 s of zips, 30 s of zips, 2 min of zips, or 4 min of zips. Males and females were transferred immediately to the refrigerator before being measured and frozen. Females were later dissected and the spermatheca placed onto a hemocytometer and covered with a cover slip so that it was compressed to a standard thickness of 0.1 mm. The spermatheca was viewed at 200× magnification. Any sperm were clearly visible through the transparent spermathecal walls. We could not make direct sperm counts because sperm could not be dispersed from previously frozen material. Instead, we obtained an estimate of the amount of sperm contained within the spermatheca by measuring its optical density using the gray scale function on the image analysis package Optimas. The gray scale ranges from 0 (black) to a maximum of 255 (white). The optical density was obtained from the log of inverse gray scale scores and is dimensionless. We determined the optical density of the spermathecal walls per se by measuring the spermathecae of virgin females. We also controlled for potential differences in sperm density due to differences in spermathecal capacity by dividing our measure of sperm density by spermathecal volume, which was determined using the area morphometry function on Optimas and the known depth of the hemocytometer. The bursa copulatrix was also mounted onto a hemocytometer and examined for sperm. The volume present was determined from its area and the depth of the hemocytometer. Testis weights of males were determined as above.

Female remating tendency

We determined the propensity for females to remate after their first copulation had either been interrupted after 1 s, 5 s, 15 s, 30 s, or 60 s or when they had been allowed to complete their first copulation without interference. First, freshly emerged females were placed in a net with a male captured at random from those patrolling the emergence site or its periphery. After a randomly allocated period of copulation, we removed the first male and immediately placed a second male with the female. The copulatory behavior of the second male was recorded as above. We also captured 10 females that had begun building nests at the emergence site and provided each with a series of three randomly captured males. Each male was held with a female and the pair repeatedly brought into contact. Pairs that failed to initiate mating within about 2 min were separated, the male discarded, and another male introduced.

We screened data to confirm underlying assumptions of parametric statistics. Where these were violated, nonparametric equivalents were used. All means are presented ±1 SE.

RESULTS

Variation in testes mass

The distribution of head widths of males used in our experiments is shown in Figure 2A. All males with head widths ≥6.3 were classified as majors, and those with head widths <6.3 were classified as minors. The distribution of male sizes is discontinuous; males of head widths between 6.1 and 6.25 are consistently rare or absent in all populations studied (Alcock, 1996b; Houston, 1991). Note that this was a nonrandom sample of the population. Among males that emerged during this study, minors represented 78% (Alcock, unpublished data).

Analysis of covariance revealed that testis mass increased with body mass ($F_{1,94} = 12.29$, $p = .0007$) but did not differ between male morphs ($F_{1,94} = 2.59$, $p = .111$). There was no body mass by morph interaction ($F_{1,94} = 0.56$, $p = .456$). The allometry of testis mass is shown in Figure 2B. Within morphs, testis mass increased with body mass with an allometric exponent <1.0 (common within morph slope $b = 0.77 \pm 0.20$).

Variation in male mating behavior

Major and minor males behaved similarly while copulating. Phase 1 lasted on average 16.2 ± 3.9 s (comparison between morphs: Mann-Whitney $U = 152$, $n = 33$, $p = .196$), and males achieved intromission after performing an average of two wing flicks (comparison between morphs: $U = 170$, $n = 36$, $p = .75$; Figure 3A). We performed a repeated-measures ANOVA on the number of zips produced within each minute of phases 2 and 3 of copulation. The rate of zips produced declined significantly over the course of copulation, but there was no difference due to male morph and no interaction between morph and time (morph: $F_{1,19} = 0.479$, $p = .497$; repeated measure (minute): $F_{5,95} = 41.891$, $p < .001$; interaction: $F_{5,95} = 0.522$, $p = .759$; Figure 3B).

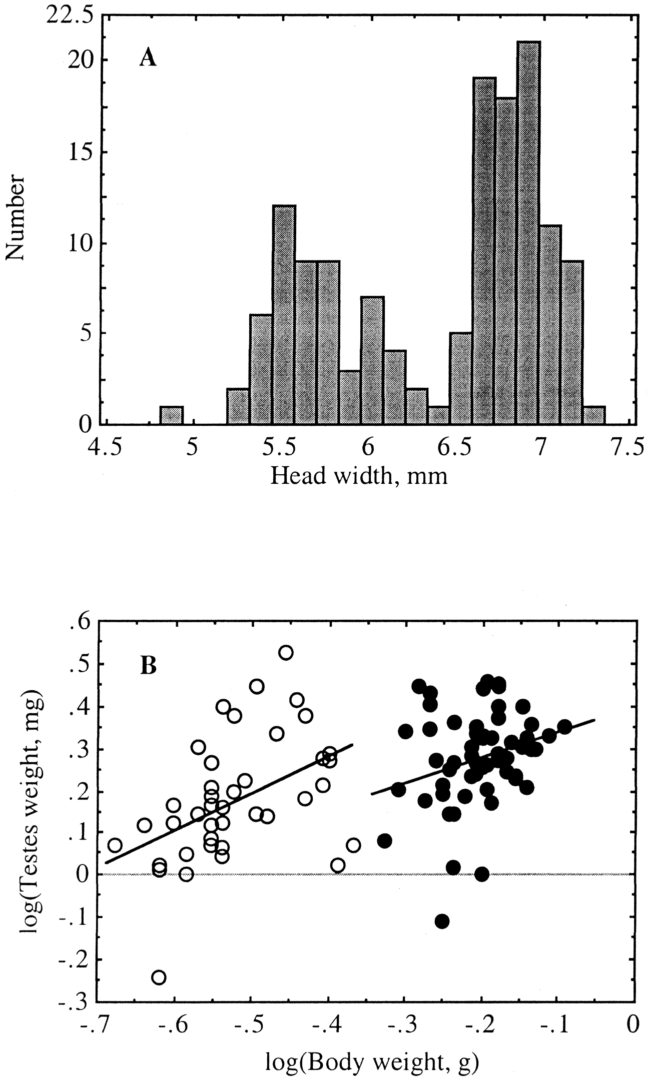

Figure 2
Morphology of male *Amegilla dawsoni*. (A) Distribution of head widths of males used in the study. Those ≥6.3 mm are majors and those<6.3 mm are minors. (B) Allometry of testes mass within minor (open symbols) and major males (filled symbols). Separate slopes are depicted although ANCOVA revealed these slopes to be homogeneous across morphs (see text).

Phase 2 ceased after 2.45 ± 0.35 min on average when the male withdrew his genitalia; mean time of withdrawal did not differ between morphs ($U = 153$, $n = 36$, $p = .552$). The morphs did differ in the number of flutters performed per minute of phase 3 of copulation (taken as minute 3 onward; see Figure 3A), with minors performing more flutters than majors (morph: $F_{1,11} = 7.35$; $p = .02$; repeated measure (minute): $F_{3,33} = .32$, $p = .81$; interaction: $F_{3,33} = 1.84$, $p = .16$). However, this difference was not significant at the experiment-wide Bonferroni adjusted probability of 0.008 (sequential adjustment with α = 0.05 for comparison of six related behavioral events). Total copula duration was 7.88 ± 0.77 min and

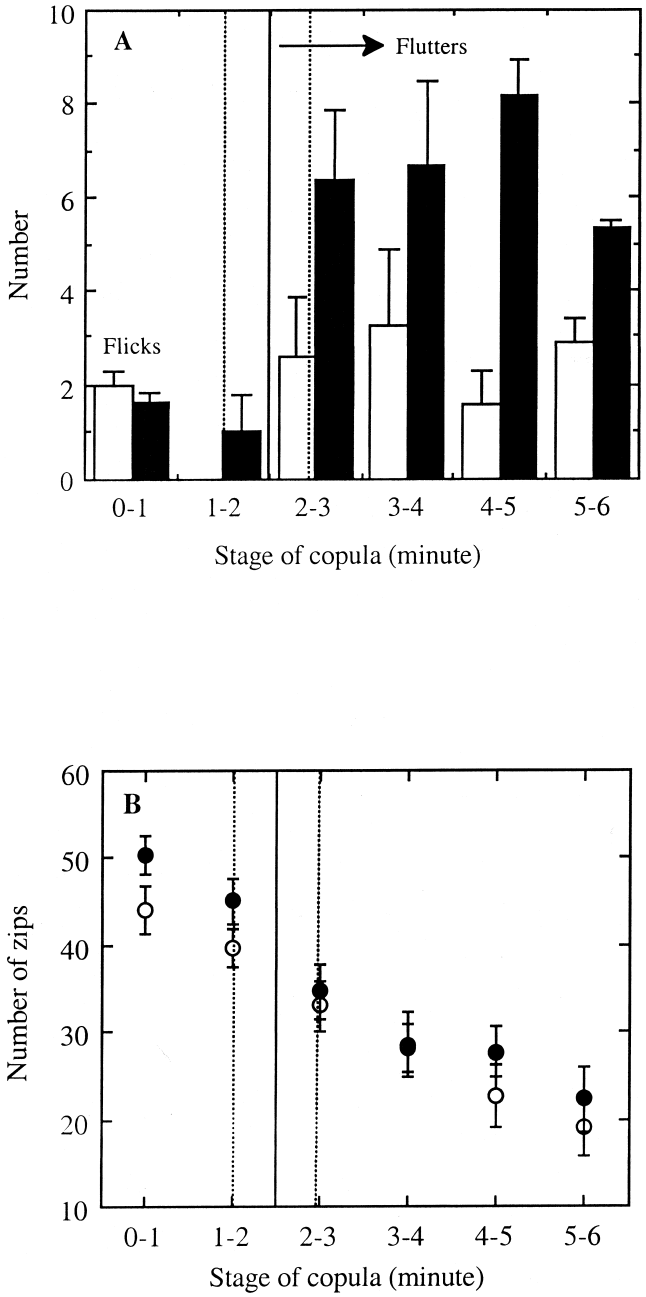

Figure 3
The mating behavior of major (open symbols) and minor (filled symbols) male *Amegilla dawsoni*. (A) The mean (±SE) number of flicks during the 16 s of phase 1 of copulation is shown in the first minute. Flutters were confined to phase 3 of copulation. (B) The number of zips during each minute of phase 2 and 3 of copulation. The vertical lines show the mean (±SE) time at which the male withdrew his genitalia and represent the average transition between phase 2 and 3 of copulation.

did not differ between morphs ($U = 191$, $n = 36$, $p = .349$). Matings observed in the net did not differ from those observed in the peripheral vegetation of the emergence site for any parameter measured [e.g., for natural matings total copula duration was 5.7 ± 0.8 min ($n = 6$) compared with matings in the net, $U = 107.5$, $n = 38$, $p = .280$; phase 2 was 2.04 ± 0.40 min ($n = 5$) compared with matings in the net, $U = 76$, $n = 35$, $p = .604$].

Variation in sperm transfer

All experimental females were found to have sperm in the bursa copulatrix, irrespective of the duration of copulation ($n = 50$). The volume of ejaculate found in the bursa copulatrix (0.69 ± 0.11 mm^3, $n = 11$) was much greater than the volume of the spermatheca ($5.31 \pm 0.09 \times 10^{-3}$ mm^3, $n = 52$), suggesting that males transfer more ejaculate than females can store. To determine how much ejaculate is transferred, we combined our data on testes weights for males that had not been allowed to copulate with those obtained from our sample of males used in experimental copulations and regressed log testes weight on log body weight as before. Residuals from this analysis showed that mated males had lighter mean residual testes weight (-0.17 ± 0.02 mg) than unmated males (0.00 ± 0.01 mg; $t = 7.47$, df = 136, $p < .001$). Thus, residual testes mass provides us with an approximate estimate of the amount of ejaculate transferred in copulation.

Among mated males, there was no relation between the duration of copulation and residual testes mass ($F_{1,38} = .008$, $p = .930$), suggesting that sperm are transferred immediately at the onset of copulation (Figure 4A). Neither was there a significant difference between major and minor males ($t = 1.35$, df = 38, $p = .186$), suggesting that males of both morphs transfer the same amount of ejaculate.

The spermatheca filled rapidly with sperm. The optical density of the spermatheca was significantly greater in mated females than in virgins because of the presence of sperm ($t = 5.07$, df = 50, $p < .001$). Moreover, the optical density of the spermathecae of mated females increased over the course of copulation ($F_{1,46} = 4.08$, $p = .049$; Figure 4B).

Female remating tendency

The probability that a female would mate with a second male (allowing intromission and entering phase 2) decreased rapidly with the duration of the first male's copulation ($\chi^2 = 36.33$, df = 5, $p < .001$; Figure 5B). The behavior of second males is shown in Figure 5. Females rarely mated with a second male if they had experienced an initial copulation that exceeded five zips (5 s in duration). When a female's first mate had performed ≤5 zips, the second male performed a normal copulation, with no differences in the numbers of flicks in phase 1 (contrasting with first male in natural copulations; Kruskal Wallis $H = 1.479$, df = 2, $p = .48$, $n = 24$; see Figure 5A) or total number of zips in phases 2 and 3 ($H = 0.08$, df = 2, $p = .961$, $n = 24$; Figure 5B).

Conversely, when a female's first mate had performed >5 zips, the second male failed to gain intromission and enter phase 2; second males performed an average of 23 wing flicks before dismounting (Figure 5A). There were two exceptions. One male gained intromission with a female that had experienced 15 s of zips, and another with a female that had experienced 30 s of zips. These males performed 8 and 55 zips, respectively, much less than in a normal copulation.

These results suggest that females are unlikely to mate more than once on emergence. Moreover, of 30 males tested in a net with 10 different females that had returned to the site to nest, none attempted to mount the female. The density of sperm in the spermatheca of nesting females did not differ from that in females experiencing a single complete copulation on emergence (nesting: 1.57 ± 0.10; once mated: 1.58 ± 0.02; $t = 0.13$, df = 37, $p = .899$). Finally, nesting females were never found with sperm in the bursa copulatrix ($n = 30$).

DISCUSSION

Do minor males exhibit adaptation for sperm competition?

The puzzle posed by the abundance of small minor males in a species in which large major males apparently experience

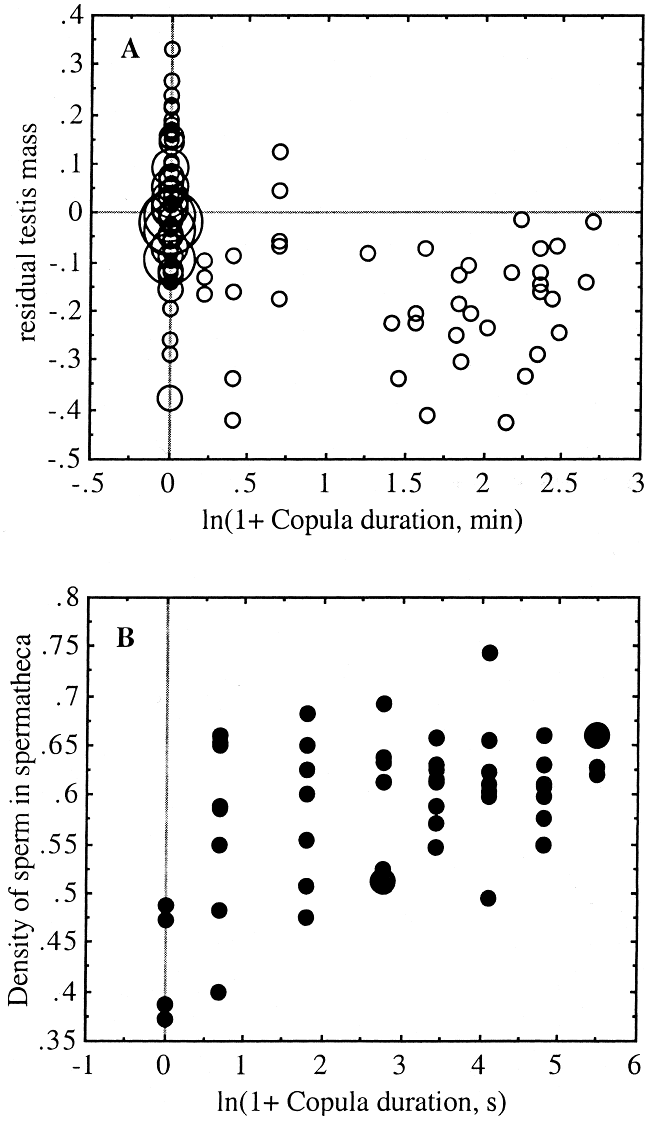

Figure 4
Sperm transfer during copulation. (A) Testes mass declined immediately upon intromission and remained constant thereafter. (B) Uptake of sperm into the spermatheca over the course of copulation indicated by the increasing optical density of the lumen of the spermatheca. Note the difference in time scale between in the two parts of the figure. Larger points represent multiple data (see text for more details).

much greater reproductive success might be partly resolved if minor males compensated for reduced access to virgins by inseminating already mated females. The sperm competition hypothesis generates the predictions that minor males should differ from major males in producing more sperm (via proportionally larger testes) or providing more copulatory courtship designed to influence cryptic female choice or transferring a greater volume of sperm. None of these predictions were confirmed.

Studies of ejaculation strategies associated with alternative mating tactics have come predominantly from research on fish. Typically, sneaker males have a higher gonosomatic index (GSI) than guarding or territorial males (reviewed in Taborsky, 1994), and this is taken as evidence for selection via sperm competition. GSI is calculated as the weight of the testes divided by body weight. The problem with GSI is that it fails to take account of allometric scaling; when traits scale with an allometric exponent <1.0, there is an a priori expectation for smaller individuals to have relatively larger traits. The allometric exponent for testis mass was 0.77. If we had calculated GSI for Dawson's burrowing bees, we would therefore have concluded that minor males invested relatively more heavily in testes. However, such a pattern is clearly not indicative of a greater investment in sperm production; the two morphs did not differ in their copulatory behavior or in the amount of ejaculate transferred per copulation. Instead, we adopted the analysis of covariance approach as recommended by Pack-

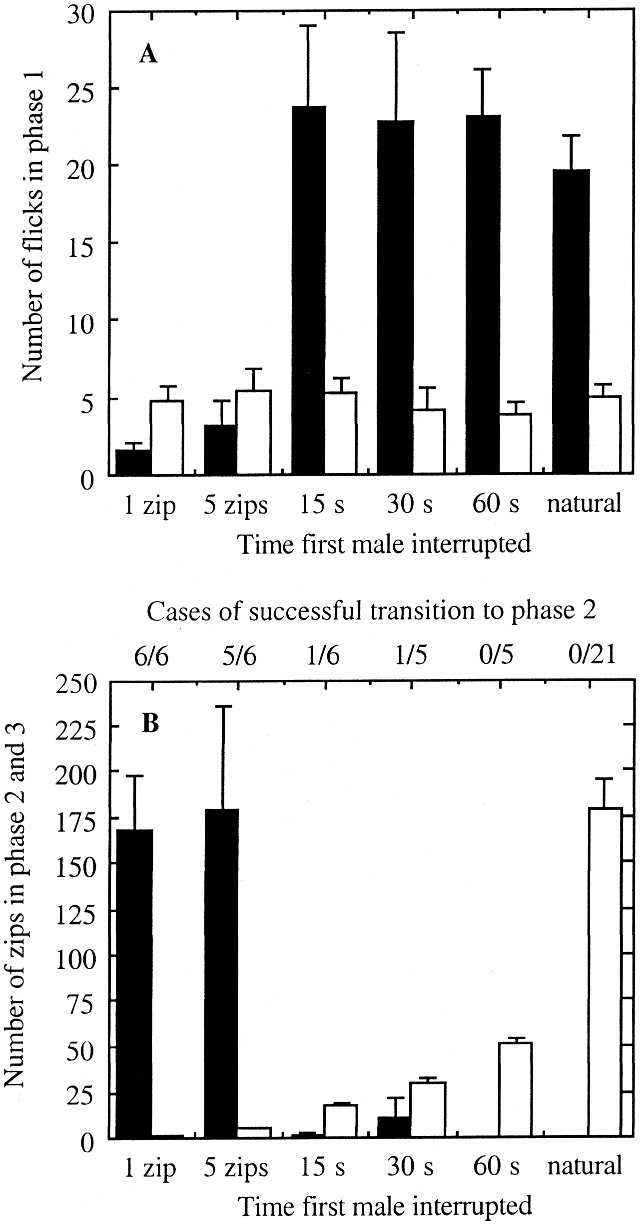

Figure 5
The mating behavior of second males (filled bars) in relation to the stage at which the female's first copulation was interrupted. The behavior of first males (open bars) is provided for comparison. "Natural" refers to an uninterrupted first copulation. (A) The mean (±SE) number of flicks during phase 1 of copulation. (B) The mean (±SE) number of zips produced by second males during phase 2 and 3 of copulation. The proportion of males achieving intromission and thus entering phase 2 is given above.

ard and Boardman (1988). This approach correctly revealed that after controlling for body mass, the two morphs did not differ in testes mass. Thus, minor males of Dawson's burrowing bee show no evidence of adaptation to sperm competition. In fish, sneakers are also typically smaller individuals who are unable to compete successfully with their larger conspecifics. Our data for Dawson's burrowing bee suggest that in general it is difficult to determine the extent to which patterns of GSI represent adaptations to sperm competition (Parker, 1990) or patterns of relative growth (Huxley, 1936), a problem recently highlighted in the study by Simmons et al. (1999) of dimorphic male beetles.

Do females tend to mate more than once?

The sperm competition hypothesis generates another key prediction—namely, that females will mate with more than one male. However, several lines of evidence suggest that female *Amegilla dawsoni* rarely mate more than once. First, our mating experiments showed that newly emerged females became highly unreceptive quickly after even a brief period of intromission. Second, females returning to the emergence site to begin nesting were also not sexually receptive, and indeed were ignored by sexually active males. Third, our dissections showed that the density of sperm in the spermatheca of females mated once under experimental conditions did not differ from the density of sperm in nesting females.

Page (1986), and more recently Boomsma and Ratnieks (1996), have reviewed the incidence of multiple mating in eusocial insects, pointing out problems associated with the available methods for assessing female mating frequencies. For example, observational data on monandry are difficult to verify because females could regain sexual receptivity some time after an initial copulation. However, we found that post-emergent females are ignored by mate-searching males, suggesting that loss of receptivity is permanent and that males are capable of recognizing and avoiding unreceptive females.

A second problem in establishing mating frequencies arises because single insemination cannot be determined by dissection data alone. Although females may have a limited storage capacity, they may still store small amounts of sperm from several different males or be subject to sperm displacement by each of their mating partners. Thus, our dissection data can only be taken as consistent with monandry. Nevertheless, recent microsatellite analysis of parentage in bumble bees (Estoup et al., 1995) has demonstrated that combined observational and dissection data (reviewed in Page, 1986) are accurate in assigning monandry in this genus. In addition, monandry is not uncommon in the Hymenoptera (Boomsma and Ratnieks, 1996; Page, 1986; Page and Metcalf, 1982) and indeed may be typical of solitary bees and wasps (Thornhill and Alcock, 1983).

Dawson's burrowing bees also exhibit a variety of life-history and behavior patterns that are consistent with monandry. Selection should favor adaptations in males that enable them to find and inseminate virgin females during their brief period of sexual receptivity. The bees show marked protandry, with males emerging some 10 days before females, on average, and are able to detect about-to-emerge females as soon as they break the soil surface (Alcock, 1997c). Strong protandry and rapid location of emerging females is a common feature of monandrous bees, wasps, and other insects (reviewed in Thornhill and Alcock, 1983).

Thus, although without molecular evidence we cannot be certain that female Dawson's burrowing bee are monandrous, the weight of evidence strongly indicates that multiple mating is rare or absent.

Copulatory and postcopulatory courtship in Dawson's burrowing bee

A striking feature of reproduction in Dawson's burrowing bee is the stereotypical behavior of males during copulation and also during phase 3, the postcopulatory period after insemination. Vibration and sound comunication in the context of courtship and copulation have similarly been reported from other solitary bees and wasps (Larsen et al., 1986). The behavior fits precisely the criteria for copulatory courtship outlined by Eberhard (1996)and has been linked with cryptic choice by females that possibly use male stimulatory performance to decide which of several males' sperm to use to fertilize their eggs. Yet, despite copulatory and postcopulatory courtship in Dawson's burrowing bees, our data suggest that females rarely mate more than once. Moreover, females do not make loss of sexual receptivity contingent upon receipt of copulatory courtship, unlike another anthophorine bee *Centris pallida* (Alcock and Buchmann, 1985). Instead, females lose their sexual receptivity within the first 5 s of copulation, long before completion of signaling by their copulatory partner but coincident with receipt of sperm inasmuch as males ejaculate into the bursa copulatrix soon after intromission has been achieved.

Although we can only speculate on the precise mechanism by which sexual receptivity is lost, our data strongly imply the involvement of the ejaculate, either via mechanical stimulation arising from the presence of sperm in the female's reproductive tract or via refractory inducing substances transferred in the seminal fluids. The fact that females became unreceptive without the extended behavioral interactions of phases 2 and 3 of copulation suggest that these phases are not directly responsible for altering female sexual receptivity. Rather, the gradual accumulation of sperm in the spermatheca suggests that the about 7 min of copulatory behavior functions in stimulating the female to transport sperm from the bursa copulatrix to the spermatheca. Permanent loss of female sexual receptivity may be contingent on sperm being transferred to the spermatheca, in which case females receiving insufficient copulatory courtship might regain receptivity some time in the future. If this were true, the presence of copulatory courtship in Dawson's burrowing bee would be evidence for cryptic female choice (Eberhard, 1996).

Although certain features of the mating behavior of Dawson's burrowing bees are incompletely understood, our data show that minor males have no obvious adaptations for sperm competition and females do not appear to mate more than once. As a result, we reject the hypothesis that success in sperm competition can compensate for the costs of producing minor sons. The reason that minor male Dawson's burrowing bee are maintaned in such high frequency must therefore remain a puzzle (Alcock, 1996b).

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