

Competition from Large Males and the Alternative Mating Tactics of Small Males of Dawson's Burrowing Bee (*Amegilla dawsoni*) (Apidae, Apinae, Anthophorini)

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Males of Dawson's burrowing bees (Amegilla dawsoni) search for virgin females at three locations: (1) open clay patches where females are emerging from underground brood cells, (2) the vegetated peripheral zone adjacent to emergence areas (through which females pass after emerging), and (3) clusters of flowering plants, which are often some distance from emergence areas. Males of Dawson's burrowing bees exhibit a size dimorphism with large major and small minors. Major males patrol only the open emergence sites, whereas minor males may be found in all three locations. Although most females are mounted and presumably mated immediately upon emergence, some are not, and these females make up a pool of potential mates for the small males patrolling the peripheral zone and flower patches. The density of males at emergence sites and the probability of male-male aggression change over the course of a day and over the entire flight season. When the level of competition is low, some minor males hunt for mates at emergence areas, where potential mates are relatively numerous. But when the presence of many large rivals makes it unlikely that a small male can avoid being displaced from emerging females, minors make the best of a bad job by shifting to areas where majors are absent.

KEY WORDS: alternative mating tactics; bees; body size; male dimorphism.

INTRODUCTION

Dawson's burrowing bee (*Amegilla dawsoni*) exhibits a bimodal size dimorphism, with large major and small minor males (Houston, 1991). Both types of males sometimes search for mates together in areas from which receptive virgin

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females can be found emerging from underground brood cells. Because males compete aggressively for strategic position by emergence tunnels containing virgin females, major males have an advantage over smaller ones, which they regularly displace from potential mates that minor males had discovered (Alcock, 1996a). As a result, majors appear to have a substantial mating advantage over their smaller rivals (Alcock, 1996b).

The maintenance of minor males of Dawson's burrowing bees in the face of their fighting and mating disadvantage offers an interesting evolutionary problem. A complete solution to the problem requires an examination of female brood provisioning decisions, since adult size is a function of the resources allocated to larvae by their mothers. The fitness gains to females from sons of different sizes is explored elsewhere (Alcock, 1996b). The main goal of the current paper is to investigate how smaller males provide as large a reproductive return as possible to their mothers, given the intensely competitive social environment in which they must operate.

Alternative mating tactics are one possible way in which small males may salvage some reproductive opportunities when competing against larger, more aggressive opponents (Dominey, 1984). Such tactics have evolved in many insects with large variation in male body size (e.g., Alcock *et al.*, 1977; Borgia, 1980; O'Neill and Evans, 1983; Ward, 1983; Crespi, 1986). In the case of Dawson's burrowing bee, I demonstrate that Houston (1991) was correct in speculating that small males of Dawson's burrowing bee patrolled areas other than the emergence site as an alternative mating tactic that enabled them to avoid major males. I also show that minor males adopt the alternative tactic only when the costs of pursuing the relatively high payoff option (searching for emerging females) are rising because of increased competition with larger males. These abilities may help minors compensate for the disadvantage they face in aggressive competition for mates with much larger males.

MATERIALS AND METHODS

The Study Sites

The bee was observed at four emergence/mating sites in Western Australia, first at Miaboolya Beach Road about 1 km from the Indian Ocean, near Carnarvon, W.A., between 27 July to 3 August 1993, from 19 July to 7 August 1994, and from 7 July to 10 August 1995. During past road construction at this site (Carnarvon 1), an area roughly 500 m² was scraped clean of vegetation down to a firm clay base. Portions of the area totaling about 165 m² have been used in all 3 years as a nesting site by many hundreds of females.

The second site (Carnarvon 2) was located about 2 km to the north of Carnarvon 1 along a dirt track. Females have regularly nested in an area roughly

72 m² and it was here that males were observed searching for mates from 25 July to 10 August 1994 and from 6 to 23 July 1995.

The third study site (Kennedy Ranges) was located on the border of a large clay pan at the eastern border of Kennedy Ranges National Park, approximately 200 km inland from Carnarvon. Many females emerged from a 420-m² area from 16 to 23 August 1993 and from 13 to 19 August 1994.

Bees at a fourth large emergence site (Ballinoo) were studied from 7 to 10 September 1993, from 21 to 29 August 1994, and from 12 August to 4 September 1995, near the Ballinoo Bridge over the Murchison River on the Mullewa-Carnarvon Road about 130 km north of Mullewa and about 500 km south of Kennedy Ranges. Here bees emerged from portions of a bare clay scrape totaling about 375 m².

Securing Samples of Patrolling Males

Below I present the results of sampling various populations of patrolling males at different locations and times. Within emergence areas, I used two techniques to gather random samples of patrollers, capturing males when they were not moving so that individuals of all sizes were equally easy to secure. One technique involved netting whatever individuals first happened to land on the ground within my reach in the emergence area. Patrolling males frequently alighted on the ground, especially during that part of the flight season when there were many open emergence tunnels to inspect. While perched, they could be captured fairly easily.

The second sampling technique was used both in the emergence area and in the peripheral zone. I first removed from a refrigerator a virgin female that I had previously captured and frozen. I placed a stout insect pin through the female and stuck the pin into the ground (in emergence areas) or into a short twig, which was then inserted into the ground (in flower patches or in the peripheral zone around emergence areas). As patrolling males found and pounced upon the female "decoy," I either picked them off by hand or placed a net over them.

The head width of captured males was measured with dial calipers accurate to 0.05 mm. Head width is a commonly used measure of body size in bees (Stubblefield and Seger, 1994) and it is highly correlated with body weight in Dawson's burrowing bee (Pearson's $r = 0.96$ for a sample of 81 males captured, measured, and then weighed on an Ohaus Portable Balance accurate to 1 mg at Carnarvon 1 from 4 to 9 August 1995). I assigned a male to the "major" group if his head width equaled or exceeded 6.3 mm. All smaller males were placed in the "minor" category. [Males with head widths of 6.0 to 6.4 were the least abundant in the male populations analyzed by Houston (1991).] Before their release, many captured males were also given distinctive marks with Liquid Paper Typewriting Correction Fluid or Humbrol Water Based Paints or small,

plastic, numbered bee tags, which were glued on the dorsum of the male's thorax.

Securing Samples of Males that Acquired Mates

Some days during the 1993 and 1994 flight seasons were devoted to collecting samples of mating males at the four sites. On these days, I arrived at the site around 0900, waited for the first mating to occur, and then captured and marked every mating male that my assistant and I could find over the next 2 to 5 h. On these same days, I also marked and measured samples of males captured as they patrolled the emergence area. I added males to these samples throughout the day so that by the end, I had captured about as many patrollers as mating males. These samples permit a comparison of the mean size of patrolling and mating males present on these days.

Measuring Competition Levels within Emergence Sites

To measure the potential for male-male competition within emergence areas, I censused the numbers of males patrolling areas at hourly intervals on 14 days in 1994 at Carnarvon 1 and 2. Censuses were made by standing back from the emergence area and scanning the length of the site while counting off males (in groups of five when populations became large).

At Carnarvon 1 and Carnarvon 2, I also gathered direct measures of male-male competition on 7 days in 1994 and on 4 days in 1995 when I hunted for as many about-to-emerge females as possible (which I did primarily by scanning for male bees waiting on the surface by an emergence tunnel). As soon as one female had been located, the spot was watched until the bee emerged while I recorded (1) the time between discovery of the site by a human observer and the departure of the female bee, (2) the occurrence of venter-to-venter wrestling by two male competitors for control of the emergence tunnel, (3) the number of males present at the spot when the female left her tunnel, and (4) the size of the male that mated with the female (if she was mounted immediately upon emergence). After completing one record, the area was scanned until the next emerging female was discovered, and so on, until 5 h had passed. From 16 to 44 emerging females were observed per day, for a total of 375 records.

RESULTS

Alternative Mate-Searching Tactics of Male Dawson's Burrowing Bees

Males of *Amegilla dawsoni* are most conspicuous when large numbers of individuals are flying slowly a few centimeters over clay pans and other similar barren clay patches from which virgin females are emerging. These patrolling

males sometimes find and mate with virgin females immediately after they exit from their emergence tunnels (Houston, 1991; Alcock, 1996a).

In addition to emergence site patrollers, both Houston (1991) and I have observed males flying within and around patches of flowering foodplants visited by females. These males travel very rapidly at heights from about 25 cm to 1 m among shrubs of *Eremophila* sp. (Myoporaceae) and tall stalks of northern bluebells *Trichodesma* sp. (Boraginaceae). Houston (1991) suggested that the rapid fliers were searching for receptive females that had flown to flowering plants after emerging. He noted, however, that foraging females were invariably ignored by passing males, indicating that receptive (virgin?) females were probably a very small minority of those present at foodplants. (No information exists on the frequency of multiple mating by females of Dawson's burrowing bees.)

I confirmed Houston's hypothesis that males cruising in foodplant patches were searching for mates by pinning dead virgin female bees to plants or sticks in places where patrollers had been seen. In patches of bluebells near Carnarvon 1 in 1993, six males were captured after they pounced upon pinned females and attempted to copulate with them. In similar flower patches in 1994 and 1995, I captured an additional 20 males as they tried to mate with female "decoys."

In addition to open emergence sites and stands of flowering plants, males also patrolled the scrubby vegetated areas immediately adjacent to barren emergence sites. Here too they flew extremely rapidly, quite close to the ground (less than 1 m high), and they attempted to mate with dead, tethered, virgin females (Fig. 1). Using the female decoy technique and sweep-netting in the peripheral zone from 2 to 5 m back from emergence areas, I captured a total of 551 males at four locations.

The behavior of males in the peripheral zone suggested that they were competing via scramble competition rather than by attempting to defend spots where receptive females might appear. I never observed peripheral males grappling with one another. Instead, they seemed to remain in perpetual high-speed flight when traveling through the peripheral zone, except when they spotted a potential mate, which elicited an abrupt halt and rapid pounce. Furthermore, when I compared the head width of the first and second males to find and mount a female decoy in a particular location, the mean head width of the first male was 5.65 ± 0.13 mm, versus 5.66 ± 0.16 mm for the second male ($t = 0.16$, paired t test, $n = 25$, $P > 0.50$). This finding offers no evidence for a large male mating advantage among peripheral males, which in turn suggests that these males were engaged in (nonaggressive) scramble competition for mates.

Males patrolling the peripheral zone were presumably searching for virgin females that had managed to leave the emergence area without having copulated with a patroller there. Recently emerged females sometimes did leave the area before mating. For example, during the 1993 study at Kennedy Ranges, when the patroller density was extremely low, I saw 13 females exit from their emer-

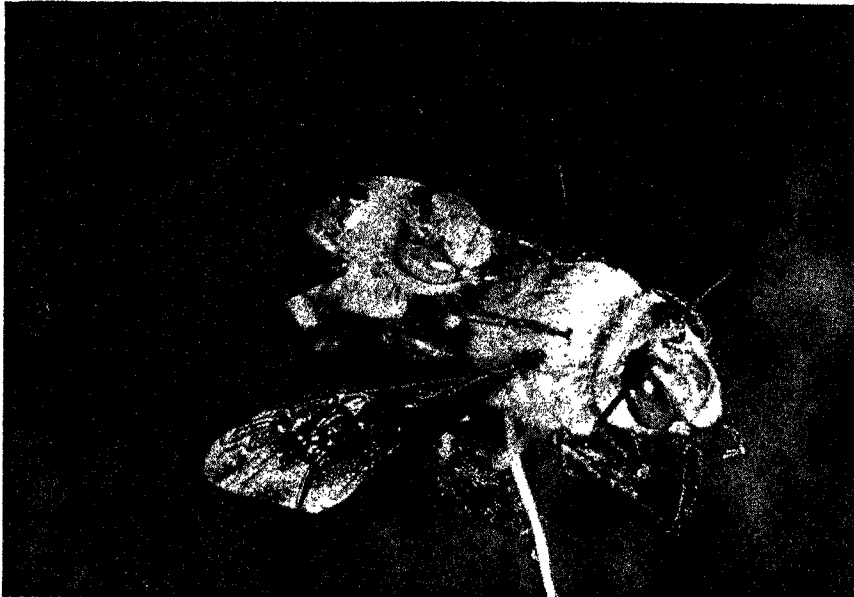


Fig. 1. A male of Dawson's burrowing bee mounted on a dead, tethered female that had been placed in the peripheral zone near an emergence site.

gence tunnels before they were detected by a male. Moreover, even when a female was discovered as she was emerging, she sometimes departed without mating. Of 375 females followed until they emerged at three study sites in 1994 and 1995, 50 (13%) flew away unmated, even though they had all been located by waiting males (Table I).

The departure of virgins occurred primarily because males waiting at emergence tunnels became distracted by male intruders, which they tried to drive off, sometimes at the cost of missing the female when she came out. Two or more males were contesting control of the emergence tunnel on 80% of the 50 cases in which a female flew off without mating. In contrast, male clashes were in progress on just 41% of the 325 cases in which the emerging female was successfully mounted by a waiting male ($\chi^2 = 25.1$, $P < 0.001$). Because some females emerged undetected and others avoided mating upon emergence when waiting males were fighting among themselves, a pool of virgin females was available to males searching for mates outside the emergence area per se.

Size and Mate-Locating Tactics

There was a strong relationship between male behavior and body size. Those individuals patrolling open emergence areas tended to be large (major)

Table 1. The Percentage of Records of Emerging Female Dawson's Burrowing Bees in Which the Female Left Her Emergence Tunnel Without Being Mounted and Mated by a Waiting Male

Site/dates	Emerging females that leave area without mating (%)
Carnarvon 1	
21, 24, 30 July and 7 Aug. 1994	23/134 (17%)
22, 25 July and 4 Aug. 1995	10/81 (12%)
Carnarvon 2	
27 July and 2 Aug. 1994	9/75 (12%)
23 and 27 July 1995	4/47 (9%)
Ballinoo	
23 Aug. 1994	4/39 (10%)
Total	50/375 (13%)

males, despite the fact that minor males predominated in samples of emerging males (Fig. 2). The difference in the proportions of minors in the samples of emerging males (66%; $n = 219$) and patrolling samples (25%; $n = 350$) gathered at Carnarvon 1 in 1995 was highly significant ($\chi^2 = 88.9$, $P < 0.001$). Outside the emergence area, all 26 males captured patrolling flowers and all but 9 (2%) of the 551 males taken in the peripheral zone were small (minor) males.

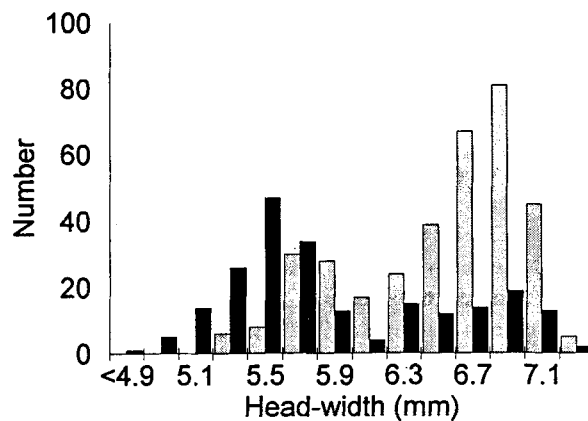


Fig. 2. The distribution of head widths of all emerging males (black bars) and patrolling males (gray bars) of Dawson's burrowing bees captured and marked at the Carnarvon 1 emergence area during the 1995 flight season. Major males have head widths equal to or greater than 6.3 mm; minors have head widths less than 6.3 mm.

Some minor males possessed the behavioral flexibility to search for females in at least two locations; over the two field seasons, I captured a total of 32 marked males (all minors) that patrolled both the emergence area and the peripheral zone (sometimes on the same day; $n = 7$).

Additional indirect evidence for behavioral flexibility by minors comes from the day-to-day changes that took place in the proportion of minors in the population patrolling the open emergence area. At some emergence sites on some days, minor males were common, although they usually constituted only a small minority of the patrollers searching for about-to-emerge females (on 14 of 20 samples at Carnarvon 1 and 2, minors made up less than one-third of the emergence area patrollers; see Fig. 5).

The relative scarcity of minors patrolling emergence areas did not stem from their overall rarity (Fig. 2). In fact, Houston (1991) concluded that minor males probably greatly outnumbered majors on the basis of a sample of dormant larvae that he excavated and weighed. I also found that minors consistently outnumbered majors by ratios ranging from 2:1 to >4:1 at six locations where I captured and measured emerging males (Alcock, 1996c).

The Effect of Changes in Male Density and Male-Male Competition

One hypothesis to account for the fluctuations in the proportion of minors in male populations patrolling emergence sites is that minors shift to the peripheral zone (or to flowering plants) as the density of major males increases. The higher the density of majors, the greater the likelihood that a minor male will lose a female he has discovered to a larger rival before he can mate with her. [Major males easily displace smaller males from tunnels containing emerging females (Alcock, 1996a).] The density-of-competition hypothesis generates the following prediction: an increase in the number of males patrolling an emergence site will lead to a decrease in the proportion of minors present in the patrolling population.

Both daily and seasonal changes occurred in the density of patrollers at emergence sites. On most days, male activity peaked around midday (Fig. 3). To test whether minor males made up a smaller proportion of the emergence-site males during the midday period, when competition for mates should be highest, I collected samples of patrollers at different times on 7 days at Carnarvon 1 and Carnarvon 2 in 1994 and 1995. As predicted (Fig. 3), minors constituted only 12% of the bees sampled during the midday ($n = 250$) while making up a larger part of the morning (51%; $n = 150$) and afternoon (46%; $n = 100$) samples ($\chi^2 = 82.3$, $P < 0.001$). Either minors left the emergence area at some point in the morning and returned later in the afternoon or minors did not come from other locations to join the patrolling population during midday when many majors did.

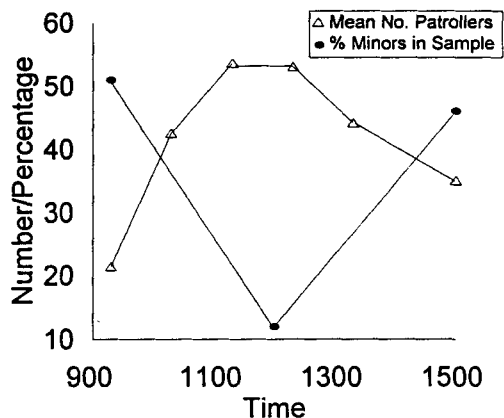


Fig. 3. The patrolling activity of minor males in relation to competition with majors. The percentage of minor males (filled circles) collected in samples made during three periods on 7 days in 1994 and 1995 at the two Carnarvon sites versus the mean number of males (open triangles) patrolling these emergence areas at different times on 14 days during the 1994 flight season.

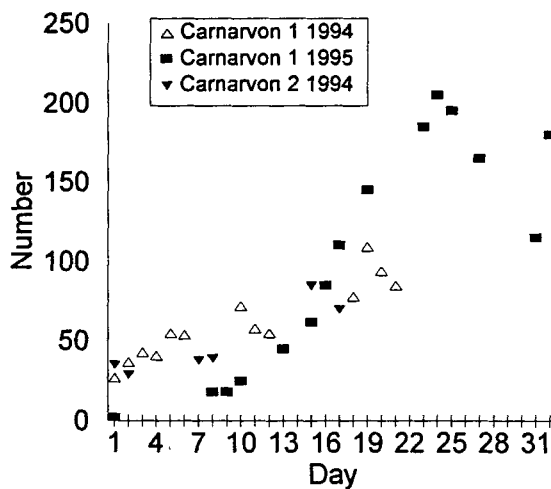


Fig. 4. Changes in the maximum number of patrollers censused on different dates during the flight seasons at Carnarvon 2 in 1994 (shaded triangles), Carnarvon 1 in 1994 (open triangles), and Carnarvon 1 in 1995 (filled rectangles).

In addition to hourly changes, there were day-to-day changes in the proportion of minors present in some emergence areas. If these changes were caused by changes in the level of competition for mates, then the proportion of minors patrolling an emergence area should fall as the overall density of male patrollers increases. Peak density on a given day provides a measure of the intensity of competition at a site. The maximum count of patrollers at a site tended to increase as the flight season progressed (Fig. 4) at Carnarvon 1 (1994 and 1995) and at Carnarvon 2 (1994). As predicted, the correlation between the maximum density of patrollers on a given day and the proportion of minors in the patrolling population (Fig. 5) was strongly negative (Pearson's $r = -0.69$, $n = 20$, $P < 0.001$).

Changes in patroller density created the potential for variation in the intensity of male-male competition at these sites. To check directly on competition levels on 11 days, I observed emerging females and recorded whether males wrestled with one another before the female left her burrow as well as the number of males present when the female came out (Table II). There was a strong negative correlation (Pearson's $r = -0.87$, $n = 11$, $P < 0.001$) between the proportion of cases in which wrestling was recorded and the proportion of females that mated with a minor male on a given day. Likewise, there was a significant negative correlation between the probability that several males would be present as the female left her emergence tunnel and the proportion of minor males in the sample of mating males (Pearson's $r = -0.77$, $n = 11$, $P < 0.01$). Thus, on days when competitors for control of emerging females were numerous and

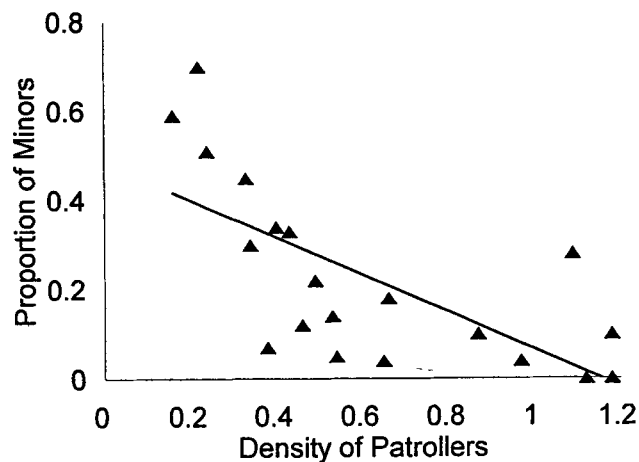


Fig. 5. The effect of changes in patroller density on the proportion of minors in the samples of patrollers collected on 20 days during the 1994 and 1995 flight seasons at Carnarvon 1 and 2.

Table II. Changes in Competition for Mates at Two Emergence Sites of *Amegilla dawsoni*: The Proportion of Records in Which (1) Wrestling Occurred Before the Emergence of the Female, (2) Two or More Males Were Present as the Female Emerged, and (3) a Minor Male Mated with the Emerging Female

Site/date	Records	Wrestling	2 or more males	Minors in mating sample
Carnarvon 1				
21 July 94	43	0.16	0.23	0.29
24 July 94	39	0.15	0.23	0.17
30 July 94	31	0.45	0.45	0.07
7 Aug. 94	21	0.81	0.86	0.00
22 July 95	18	0.72	0.67	0.00
25 July 95	37	0.84	0.76	0.00
4 Aug. 95	26	0.92	0.62	0.00
Carnarvon 2				
27 July 94	31	0.39	0.52	0.04
2 Aug. 94	44	0.52	0.52	0.06
23 July 95	16	0.88	0.63	0.00
27 July 95	30	0.80	0.63	0.00

fighting among males was commonplace, minors were less well represented in the population of mating males.

If minor males can select the mate-locating option that is likely to yield the highest reproductive payoff for them, we would expect there to be a positive correlation between the proportion of minor males in the males patrolling emergence areas and their abundance in the subpopulation of mating individuals at these locations. As Fig. 6 shows, there was indeed a close match between the proportions of minor males in the patrolling and mating samples gathered on 16 days at Carnarvon 1 and 2 (Pearson's $r = 0.93$, $n = 16$, $P < 0.001$). This finding suggests that minors can assess the intensity of competition for mates in an emergence area and will remain only if they have about the same chance of mating as their larger rivals.

DISCUSSION

Body Size and the Choice of Mate-Location Sites

Dawson's burrowing bee is an insect in which body size dramatically influences male mate-locating tactics. First, larger males of Dawson's burrowing bee patrol only areas where emerging females can be found, whereas minor males possess the behavioral flexibility to search within emergence sites, or in the region immediately surrounding these sites, or at patches of flowering food-plants. This pattern occurs in other members of the Anthophorini (Alcock *et*

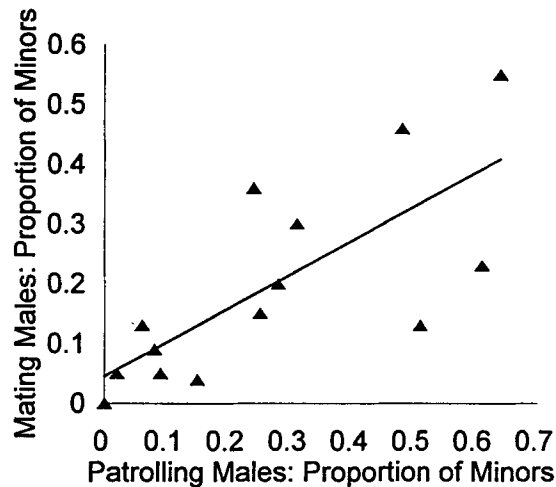


Fig. 6. The proportion of minors in samples of males mating on 16 days at Carnarvon 1 and 2 is strongly correlated with the proportion of minors in the matched samples of patrolling males collected on these days.

al., 1977; Barthell and Daly, 1995). For example, large males of *Centris pallida* search only for emerging females; smaller males sometimes join them in emergence sites, but at other times they move away to attempt to acquire mates elsewhere. One alternative tactic of these smaller individuals is to hover by shrubs on the periphery of emergence areas; from these hovering stations, small males pursue and capture some unmated females that have left their emergence tunnels without being grasped by large males (Alcock *et al.*, 1977).

Likewise in the sand wasp *Bembicinus quinquespinosus* larger males compete aggressively for females that are in the process of emerging, while small males perch in the strip just outside the emergence area, where they chase passing females and attempt to mate with them (O'Neill and Evans, 1983).

Similarly, large males of the dung fly *Scatophaga stercoraria* aggressively compete for females on the surface of dung pats (Parker, 1970; Borgia, 1980), whereas smaller males patrol the peripheral zone in the grasses around the pats attempting to intercept females moving to or from the dung (Sigurjónsdóttir and Snorrason, 1995).

Body Size and the Timing of Mate-Locating

In Dawson's burrowing bee, male body size influences not only whether a male searches for mates within or outside of emergence areas, but also when a male engages in mate-locating. Minor males patrol emergence areas earlier and

later in the day than the typical major (Fig. 3), just as is true for small males of *B. quinquespinosus* (O'Neill *et al.*, 1989).

Dawson's burrowing bee is a cool-weather, winter-active species. The readiness of small males to fly at lower temperatures than large males occurs even though large bees usually warm up more quickly (May, 1976; Stone and Willmer, 1989) and maintain higher body temperatures under cool conditions (e.g., Larsson and Tengo, 1989; Stone *et al.*, 1995). Thus, the relative abundance of small males of Dawson's burrowing bees at emergence sites early on cool winter days in Western Australia probably requires that they overcome a thermoregulatory handicap to patrol for mates before larger rivals. The benefit they derive by timing mate-searching to occur early (and late) in the day presumably is related to the relative scarcity of patrolling large males at these times.

Body Size, Fighting, and Small Male Options

A third important difference between the mating tactics of major males and those of minor males of Dawson's burrowing bees is the readiness of major males to fight rivals for access to emerging females, whereas minor males in the peripheral zone engage in purely nonaggressive scramble competition for flying virgin females. The correlation between large body size and fighting is standard among insects in which there are substantial differences in male body size and alternative male mating tactics (e.g., Thornhill and Alcock, 1983; O'Neill *et al.*, 1989; Danforth, 1991; Polak, 1993; Rasmussen, 1994). The typical pattern is one in which large, fighting males exploit a high-cost, high-payoff option, whereas small males that avoid aggression adopt a low-cost, but low-payoff alternative. Thus, for example, large males of the sand wasp *Bembicinus quinquespinosus* appear to succeed in finding and mating with most emerging females, leaving smaller males with a very small pool of virgin females that depart from the emergence area without mating (O'Neill and Evans, 1983).

This same pattern applies to Dawson's burrowing bee. Large males claim the prime mate-locating areas (emergence sites) and they aggressively monopolize virgin females during the midday hours when most females emerge. Small males that search for mates in emergence areas tend to do so only when few major males are competing with them, but at these times few virgin females are available. At other times, minors tend to be forced into peripheral areas to compete among themselves for a small fraction (13% in this study) of emerging, virgin females that evade major males. Since minors almost certainly greatly outnumber majors, the average mating success of minors hunting outside of emergence areas must be much less than that for majors patrolling within these much more productive locations.

In this and other examples (e.g., Thornhill, 1981; Eberhard, 1982; Goldsmith, 1987; Rasmussen, 1994), the dominating, aggressive behavior of large males appears to force the smaller or otherwise competitively disadvantaged

individuals into lower payoff options. If large body size consistently produces a competitive advantage, as it appears to do in Dawson's burrowing bee, the largest individuals need not possess the capacity to switch tactics, since they can always pursue the mate-locating tactic with greatest fitness returns.

Thus, as is generally true for insects and other animals (West-Eberhard, 1979; Andersson, 1994; Gross, 1996), the alternative tactics of Dawson's burrowing bees appear to be the product of one conditional strategy with unequal payoffs (Dawkins, 1980), rather than representing two genetically distinct strategies with equal fitness payoffs. Minor males that search for mates in the peripheral zone are almost certainly making the best of a bad situation. When the density of rivals in emergence areas is relatively low, some minors can profitably adopt the option with the highest potential payoff by patrolling emergence areas where receptive virgins can be contacted. But as the density of males patrolling these sites increases and majors become more numerous, the pool of about-to-emerge females available to minor males declines, resulting in a shift by many small males to alternative options, including patrolling the periphery of emergence area, where there are virtually no interfering large males. Although the mating chances of a peripheral minor are low, their opportunities within an emergence site swarming with many majors are almost certainly lower still.

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