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## Brood-provisioning strategies in Dawson's burrowing bee, *Amegilla dawsoni* (Hymenoptera: Anthophorini)

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**Abstract** Males of Dawson's burrowing bee are dimorphic in size. Although large (major) males defeat smaller ones in competition for emerging females and therefore are more likely to mate, majors are greatly outnumbered by half-sized (minor) males. Nesting females might produce many minor males, despite their low reproductive value, because female behaviour is governed by a mixed evolutionarily stable strategy (ESS), in which case the ratio of majors to minors should not be affected by changes in female condition. In contrast, a conditional-strategy hypothesis predicts that older, wing-worn or stressed females unable to forage efficiently should be especially likely to produce minor offspring, which require less brood provisions. To test these alternative hypotheses, we manipulated the condition of nesting female bees by the addition of weights and the removal of their wing margins. These manipulations, done early in the flight season, failed to increase the production of minor males, a result consistent with the mixed-ESS hypothesis. However, unmanipulated females were far more likely to produce minor males if they were small or if they were nesting late in the season, when foraging conditions had deteriorated, findings that are consistent with a conditional provisioning strategy. Thus it appears that the abundance of minor males is the result of a conditional provisioning strategy of nesting females, which may be superimposed on a fixed tendency to produce large offspring early in the season and small ones later.

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### Introduction

*Amegilla dawsoni* is a large (ca 0.5–0.7 g), univoltine, ground-nesting, solitary bee that nests in dense aggregations in clay pans in central Western Australia (Houston 1991). Nesting females produce both large (major) and small (minor) sons, a male size dimorphism that is associated with alternative mating tactics (Houston 1991; Alcock 1996a, 1997a). Major males patrol slowly over emergence sites, searching for burrows from which virgin females are about to emerge and fight with other males to control the site of emergence long enough to capture and mate with the female when she appears (Alcock 1996b). Minor males are capable of searching for emerging females but they typically avoid direct competition with majors. Many minor males fly at high speed around the periphery of emergence sites, trying to intercept virgin females that have not mated with a male immediately upon emergence (Alcock 1997a, 1997b).

Similar male dimorphisms linked with distinctive mating behaviours occur in a host of vertebrate and invertebrate taxa (e.g. Gadgil 1972; Shuster 1989; Gross 1991; Clark 1997) including such insects as earwigs (Eberhard and Gutierrez 1991; Tomkins and Simmons 1996), thrips (Crespi 1988), fig wasps (Cook et al. 1997), and assorted beetles (Eberhard 1982; Goldsmith 1985) as well as some bees (Houston 1970; Danforth 1991; Danforth and Desjardins 1999). These morphological and behavioural dimorphisms raise evolutionary questions about the origins and maintenance of the distinctive traits (e.g. Danforth and Neff 1992; Emlen and Nijhout 2000). One key question is how two alternative phenotypes can coexist over time in the face of selection, especially in those cases in which the larger or largest morph has a clear reproductive advantage (Gross 1996). In most of these instances, however, the differences between males are not hereditary but result from environ-

mental differences, especially differences in the amount of food consumed by developing individuals (e.g. Emlen 1994; Tomkins 1999). The behaviour of the smaller phenotypes in these cases is the product of a conditional strategy in which non-aggressive tactics enable them to salvage some reproductive success in the face of aggressive, larger rivals that can easily defeat them in direct contests for females (Gross 1996; Emlen 1997; Moczek and Emlen 2000).

However, when male size differences arise because of parental provisioning decisions, as is the case for male dimorphisms among bees, a new evolutionary puzzle arises: why do females provision their nests in such a way as to produce smaller, disadvantaged males that supply a small reproductive pay-off to the parent? This question applies to *A. dawsoni*, because minor males are extremely common despite their very low reproductive success relative to their larger rivals. Major males mate with an estimated two-thirds of all virgin females, which mate only once (Alcock 1996a; Simmons et al. 2000). Because minor males outnumber major males by at least 2:1, and perhaps as much as 4:1 (Alcock 1996a), the average mating success of minors can be no more than one-quarter that of majors. Although the average minor weighs about half that of an average major, and so can be estimated to cost its mother half the provisioning time of a major, data on mating success suggest that minors are overproduced by a factor of at least two and perhaps as much as four.

The costs of producing a major are possibly underestimated when one considers only the number of provisioning trips that the female bee needs to make to secure the resources for her offspring. Parasites are believed to affect parental allocation of resources by some bees (e.g. Martins et al. 1999) and brood cells of *A. dawsoni* are targeted by a parasitic miltogrammine fly. However, the fly does not seem to differentially target brood cells with resources for larger offspring (Alcock, in press). Nevertheless, some other factors still to be examined (see Rosenheim et al. 1996; Yanega 1996) could conceivably generate size-dependent investment costs such that females do gain equal fitness returns per unit investment from either a minor or a major, assuming that minors are actually much less expensive (or majors much more expensive) than they seem to be. Under these circumstances, nesting females could be employing a mixed evolutionarily stable strategy (a mixed ESS) such that they produce major and minor sons at a fixed, fitness-maximizing ratio. This hypothesis generates the key prediction that the ratio of minor to major males should be unperturbed by experimentally induced changes in female foraging capacity or by natural changes in foraging conditions over the nesting season.

An alternative hypothesis assumes that minors do not provide the same return on parental investment as majors, but that small sons are the result of a conditional provisioning strategy with two tactics, one that results in majors and the other that enables females to make the best of a bad situation. This hypothesis does not require

that both classes of sons yield equal fitness per unit of provisioning effort. The conditional-strategy hypothesis does require that experimental or natural declines in female foraging capacity (such as advancing age or increases in wing damage; Rodd et al. 1980; Neukirch 1982; Cartar 1992) or naturally occurring decreases in resource availability will result in decreased production of the more costly type of offspring (Myers 1978; Torchio and Tepedino 1980; Kim 1999).

We manipulated the brood provisioning behaviour of female *A. dawsoni* and observed the nesting behaviour of unmanipulated females over an entire season in order to test the mixed-ESS and conditional-strategy hypotheses. We report the results of this work below.

## Methods

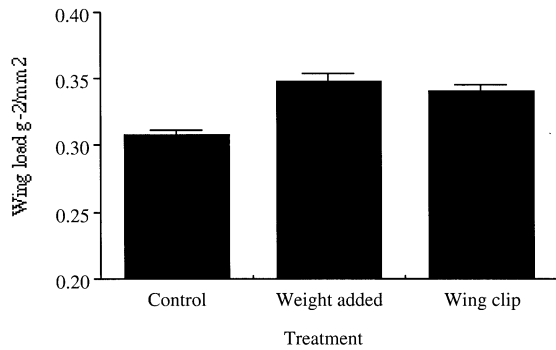
### Measuring the effects of manipulations of female condition

The study was conducted between 27 July and 7 September at a large nesting/emergence site of Dawson's burrowing bee located just off the Miaboolya beach road about 10 km north of the town of Carnarvon, Western Australia. Early in the flight season, we attempted to manipulate female foraging efficiency by capturing female bees and assigning them to one of three classes: controls, wings clipped, or weight added. The bees were captured in 50-ml plastic vials, which were placed over the burrow entrance after the bee had entered; when the bee subsequently left the burrow, it flew up into the vial, which was placed in a refrigerator in a field vehicle.

When torpid, the bees were weighed on an Ohaus portable balance accurate to 0.01 g. Female weight measured over 2 consecutive days was significantly repeatable, i.e. the variance among individuals was significantly greater than the variance within individuals ( $F_{47,46}=8.38$ ,  $P=0.0001$ ) such that the difference per female averaged 2.87% of their total weight. Bees assigned to the wing-clipped category then had a 1-mm strip of the posterior margin of the forewing removed with a pair of nail clippers, after which they were paint marked on the thorax. Weight-added bees had a small piece of lead glued to their thorax with super glue (for a sub-sample of 20, mean weight added= $0.10\pm 0.01$  g, mean weight of bees= $0.579\pm 0.01$  g; 17.5% body weight added). Control bees were also marked on the thorax with paint. The wing wear of each bee was scored according to the damage to the posterior wing margin following (Alcock 1996a). After marking or manipulation, bees were placed in the sun to warm up before being released.

The area of the fore- and hind-wings were taken from a sub-sample of collected females – 29 controls, 29 weight-added and 30 wing-clipped bees – and measured using OPTIMAS image analysis software. Wing loading was calculated as the weight of the bee (and its lead weight where applicable) divided by the bee's total wing area. The manipulations significantly increased the wing loading of the bees in the weight-added and wing-clipped treatments by about 12% (ANOVA,  $F_{2,85}=16.30$ ,  $P<0.001$ ; control vs wing clipped Tukey-Kramer HSD= $0.0149$ ,  $P<0.05$ ; control vs wing clipped HSD= $0.022$ ,  $P<0.05$ ; weight-added vs wing clipped HSD= $-0.010$ , NS; Fig. 1).

To determine whether female condition affected the duration of their pollen- and nectar-foraging trips, we first collected baseline information on trip duration. Once an unmanipulated pollen-laden bee entered her nest, a plastic vial was placed over the entrance. When the female exited the burrow into the vial, the time was recorded, the female released, and the vial replaced. When the female returned from her foraging trip, she hovered in front of the vial, which was removed to permit her to enter her nest. The time of entry was recorded and the procedure duplicated for another provisioning trip before individuals were selected for the experiments already described. Following a female's return to the bur-



**Fig. 1** Mean±SE wing loading of bees in the three treatment groups. Controls differed significantly from both wing-clipped and weight-added treatments

row after she was wing clipped, or received a weight, or became a control, the duration of her next two provisioning trips were recorded to determine the effect of the procedures on female foraging behaviour.

In addition to measuring the time taken to complete foraging trips, we also measured the weight of brood provisions brought to the nest by the various samples of females. The technique involved capturing a female as she returned from a foraging trip, which was accomplished by pushing a small piece of sponge (2 cm<sup>3</sup>) on a length of thin string about 5 cm down the burrow as the female waited to dive into it. When she was permitted to enter, a vial was placed over the entrance. Upon encountering the blocking sponge, the bee backed out into the vial and could be collected and weighed. When released, the female returned to her unblocked nest where she deposited her provisions before being captured again in a vial as she left the nest; the female was then weighed without the pollen and nectar she had just unloaded in a brood cell. The difference between the bee's weight with and without provisions yielded data on the mass of materials the female had brought to her brood cell.

Under the conditional strategy hypothesis, the experimental manipulations of wing clipping and weight addition were expected to affect the size of the offspring produced. We determined the size of the offspring a female would produce indirectly, by measuring the volume of the brood cell she built. Brood cell size is strongly correlated ( $r=0.82$ ) with the weight of the prepupa (Alcock 1999), showing that female bees construct their brood cells in anticipation of the quantity of brood provisions that they intend to bring to the cell. To measure the volume of the brood cell, we determined when a female began to dig a new chamber, which required the female to push freshly excavated, moistened soil out of her burrow entrance. When fresh dirt was observed, we continued to monitor activity at the nest at intervals to determine when the female first began to provision the new cell with pollen. At this point, the female was captured and the burrow filled with casting plaster. The site was then numbered for later excavation and the retrieval of the cast of the burrow with its filled terminal brood cell. When the waxed lining of the brood cell was picked away from the plaster, the result was a clean smooth cast of the interior of the cell. Cell dimensions were measured using Mitutoyo digital calipers accurate to 0.01 mm. The distance from the base of the cell to the neck (a clear constriction in all pots) and the widest point of the cell were measured. Cell volume was calculated as an ovoid using the formula  $\frac{4}{3}r^2 \times \frac{h}{2}$  in which  $r$  is the radius and  $h$  is the height (Speigel 1968).

Measuring changes in brood provisioning by unmanipulated females over the nesting season

Females foraged on large northern bluebells (*Trichodesma* sp.), which occurred in scattered patches around the nesting site. The

number of flowers and buds of haphazardly selected plants were counted over the course of the season to document seasonal declines in the availability of provisioning resources.

To determine if female provisioning tactics changed during the nesting period, we collected two provisioning trip times for samples of unmanipulated females on 27 and 28 July, 2, 9, 16, 26, 31 August, and 1, 6, and 7 September. These two trips were used to calculate a mean provisioning trip duration for each female. The change in trip duration over the season was estimated using these mean provisioning trip times as well as the means for the two trips that experimental females made *prior* to their experimental manipulation on 3–5 August.

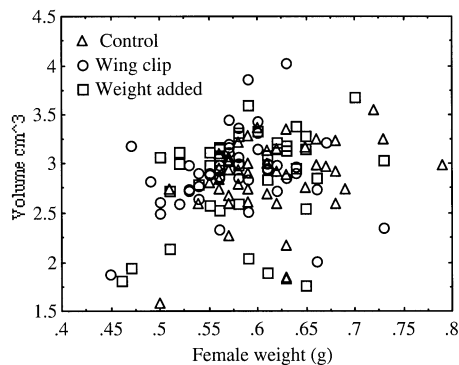
The weight of pollen and nectar loads carried by samples of unmanipulated females was also gathered over the course of the season in the manner described previously. The repeatability of female provisioning loads was estimated by recording these loads for the same marked females on consecutive days.

If there were seasonal changes in the allocation of resources to offspring made by females in response to decreased foraging success, then the mean brood cell volume was expected to decline over time. To test this prediction, we also made casts of the nest tunnels and newly dug brood cells of samples of unmanipulated females on 17, 24, 25, 31 August and 1 and 7 September. These burrow casts were excavated in October when all of the parental generation had died and their offspring were dormant prepupae. The excavation of the cast tunnels exposed many prepupae, which were collected and weighed. The prepupae in the brood cells directly beneath the cast tunnel were assumed to have been produced by the female whose burrow we had cast, enabling us to identify (tentatively) the sequence of offspring types that the female had produced. Staining techniques (Duchateau and Van Leeuwen 1990) to sex the prepupae failed because the prepupal cuticle was impermeable to the stain.

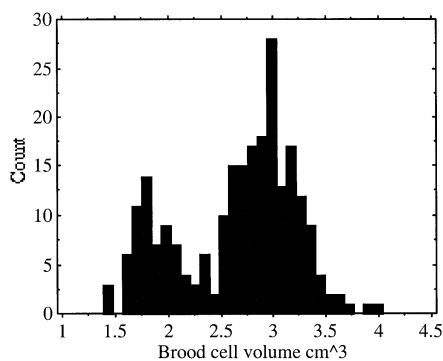
## Results

### Effects of experimental manipulations of female condition on provisioning behaviour

Data collected prior to experimental manipulations demonstrated that the variance in duration of consecutive provisioning trips was greater between females than within two trips of one individual ( $F_{73,74}=3.027$ ,  $P=0.0001$ ). This was also true following the manipulations (controls,  $F_{16,17}=2.61$ ,  $P=0.03$ ; wing clipped,  $F_{14,15}=4.63$ ,  $P=0.003$ ; weight added  $F_{10,11}=16.03$ ,  $P=0.0001$ ). Therefore, provisioning trip duration can be considered a behavioural characteristic of individual females. The impact of the three treatments on female provisioning trip duration was measured as the difference between the mean duration of the two provisioning trips prior to manipulation and the mean duration of the two trips following the manipulation. This effect of treatment was analysed with an ANOVA (date and female weight did not correlate with provisioning time and were not entered into the model). Although the treatment variances were homogeneous, they increased with the mean trip duration, and therefore data were  $\log_{10}$  transformed (after 10 had been added to remove negative numbers greater than 1). There were no significant effects of either treatment on provisioning trip duration:  $F_{2,52}=0.930$ ,  $P=0.40$ ; untransformed mean±SE change in provisioning trip time: controls,  $2.11 \pm 0.58$  min,  $n=29$ ; wing clipped,  $3.39 \pm 2.18$  min,  $n=14$ ; weight added,  $2.44 \pm 1.97$  min,  $n=12$ .



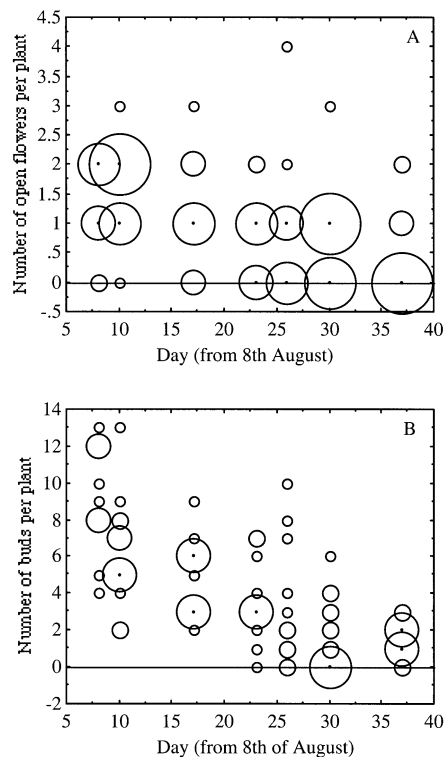
**Fig. 2** Brood cell volumes plotted against female weight in the three treatment groups. There was a positive relationship between female weight and brood cell volume (see text) but there was no difference between treatments in the production of minor (<2.25 cm<sup>3</sup>) brood cells



**Fig. 3** The bimodal distribution of brood cell volumes, with a smaller peak of minor males to the left of the major male/female peak

However, wing-clipped females brought back less provision mass than females in the other two groups:  $F_{2,37}=3.83$ ,  $P=0.03$ ; mean $\pm$ SE (g): controls,  $0.100\pm 0.01$ ,  $n=13$ ; wing clipped,  $0.065\pm 0.011$ ,  $n=15$ ; weight added,  $0.101\pm 0.012$ ,  $n=12$ . Post hoc tests showed significant differences between control and wing-clipped females (Fisher PLSD=0.0321,  $P<0.05$ ) and between weight-added and wing-clipped females (Fisher PLSD=0.0315,  $P<0.05$ ), whereas there was no significant difference between the weight-added and control treatments (Fisher PLSD=0.0326,  $P>0.05$ ).

The experimental manipulations had no significant effect on brood cell volume [least-squares mean $\pm$ SE (cm<sup>3</sup>) based on an ANCOVA with treatment as the main effect and female weight as a covariate: control,  $2.83\pm 0.06$ ,  $n=50$ ; wing clipped,  $2.95\pm 0.07$ ,  $n=48$ ; weight added,  $2.90\pm 0.06$ ,  $n=41$ ;  $F_{2,130}=1.050$ ,  $P=0.35$ ]. Female weight did have a significant positive effect on brood cell volume ( $F_{1,130}=10.304$ , pooled slope= $2.02\pm 0.63$   $P=0.002$ ; Fig. 2), but the interaction between treatment and female weight was not significant ( $P=0.614$ ), and was removed from the model. The distribution of brood cell volumes was not normal, and not normalised by log transformation. However, the hypothesis that the treatments affect-



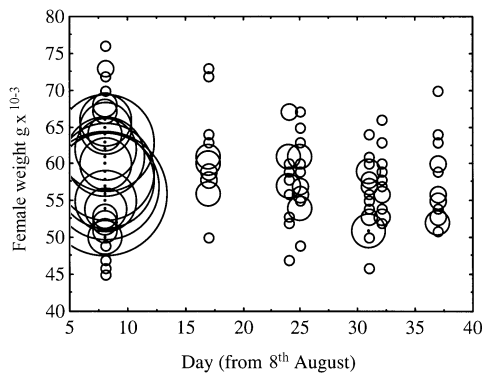
**Fig. 4** Declining resource abundance through the season, measured as the numbers of flowers per plant (A) and the numbers of buds per plant (B). Larger circles represent data points which overlap

ed brood cell size can be tested solely within the substantial data set available for large brood cells, built for large sons or daughters, whose weight distributions overlap almost completely (see Fig. 10 in Alcock 1999). This analysis confirms that manipulative treatment had no effect ( $F_{2,118}=1.912$ ,  $P=0.151$ ) whereas female weight did have an effect ( $F_{1,118}=7.347$ ,  $P=0.008$ ).

The bimodal distribution of plaster cast brood cell volumes (Fig. 3) reflects the existence of one group of small brood cells that were surely designed for minor males and another group of much larger brood cells that nesting females constructed to accommodate sufficient brood provisions for major males or females. If we assume that cells for majors/females had brood cell volumes greater than 2.25 cm<sup>3</sup> whereas cells for minors had volumes less than 2.25 cm<sup>3</sup> (mean of majors and females= $2.93\pm 0.02$ , minors= $1.84\pm 0.036$ ), then there was no difference in the ratio of minor brood cells to major/female brood cells across the treatments (minors:major/females: controls, 4:46; wing clipped, 2:44; weight added, 6:35;  $\chi^2=3.11$ ,  $df=2$ ,  $P=0.21$ ).

#### Changes in brood provisioning over the nesting season

As the nesting season progressed, resource availability declined as seen in decreases in the number of open flowers ( $r=-0.345$ ,  $n=95$ ,  $P=0.0001$ ; Fig. 4A), and the



**Fig. 5** Scatterplot of the decline in female weight over the nesting season

number of buds per bluebell plant ( $r=-0.679$ ,  $n=95$ ,  $P=0.0001$ ; Fig.4B). Female wing condition also declined, with a significant increase in wing wear over time ( $F_{1,241}=122.4$ ,  $r^2=0.334$ ,  $P<0.0001$ ). Moreover, the weight of nesting females also fell over the course of the season ( $F_{1,238}=10.05$ ,  $r^2=0.0361$ ,  $P=0.002$ ; Fig. 5). To determine if this change in weight was a result of size-related mortality or because individuals lost weight, the relationship between head width (of a subsample of females collected over the season) and date was examined. Females nesting later in the season were smaller than those nesting earlier in the season ( $F_{1,115}=9.128$ ,  $r^2=0.0654$ ,  $P=0.003$ ). The decline in female size appears to arise both from a reduction in the number of large females present and from an increase in the number of smaller females nesting. This suggests that larger females tend to emerge earlier in the season and hence die earlier, while smaller females emerge later and are therefore more common in the population later in the season.

Multiple regression allowed determination of the independent influences of female weight, date and wing condition on the provisioning trip duration of the females in the study (wing condition correlated strongly with date and so the residual wing condition, controlling for date, was used). There was no significant partial regression between residual wing wear and provisioning trip duration (Table 1), whereas significant partial regressions revealed that both female weight and the date of the sample affected provisioning trip duration (Table 1). Not all females were scored for wing wear, and an analysis of a larger data set excluding this variable yielded no significant effect of female weight (Table 1), but a strong positive relationship between provisioning trip duration and date (Table 1). As the season progressed, females took longer to return with their brood provisions.

The weight of pollen and nectar carried by female bees over 2 consecutive days was repeatable, i.e. the variation among individuals was greater than the variation within individuals ( $F_{45,46}=2.076$ ,  $P=0.008$ ) with the difference for a given female averaging 28.2% of the weight carried. There was a significant positive relationship between female weight and provisioning load, but

**Table 1** Two multiple-regression analyses: model 1, analyses the effect of date, female weight and wing condition on the mean provisioning trip times of female bees. The second model analyses a larger data set that includes females whose wing condition was not scored. Tests are robust to Bonferroni correction for the two tests on the same data set

Source	Coefficient	df	F	P
Model	5.54±3.19	3	15.3	0.0001
Date	0.593±0.09	1	42.27	0.0001
Female weight	14.05±5.19	1	7.33	0.0081
Wing condition	-0.468±0.31	1	2.29	0.1337
Error		92		
Model	9.26±3.19	2	111.418	0.0001
Date	0.33±0.02	1	222.56	0.0001
Female weight	7.26±5.27	1	1.899	0.1701
Error		163		

there was no effect of date on provisioning load (the interaction term was non-significant and was removed from the model; whole model  $F_{2,146}=5.926$ ,  $P=0.003$ ; female weight,  $\beta=0.178\pm0.053$ ,  $F_{1,146}=11.494$ ,  $P=0.0009$ ; date,  $\beta=0.000\pm0.000$ ,  $F_{1,146}=1.296$ ,  $P=0.25$ ). During the provisioning cycle, some females returned to their burrows without pollen. There was no difference in the weight that was being carried (i.e. the difference in the weight of entering versus leaving females) by bees arriving with pollen attached to their legs (mean±SE in  $g=0.1377\pm0.003$ ,  $n=148$ ) and those entering without pollen ( $0.1312\pm0.005$  g,  $n=67$ ,  $df=214$ ,  $t=1.11$ ,  $P=0.26$ ), either because the pollen-free bees were carrying extra nectar or because pollen weighs very little.

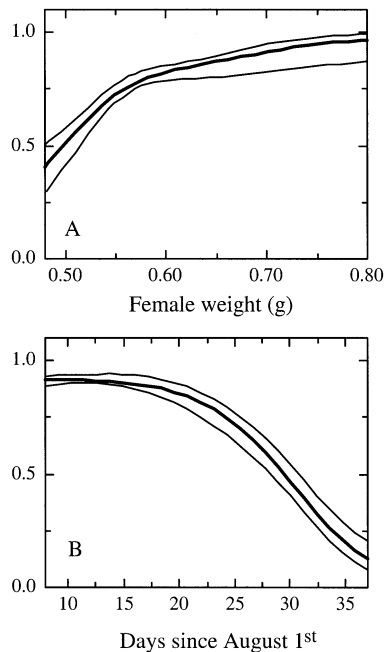
The data on brood cell size can be analysed both in terms of the continuous variable of brood cell volume and in terms of the discontinuous variable of brood cell type (major male/female or minor male). We have used both approaches. The changes in volume were analysed in a multiple regression with date, female weight and residual wing wear (wing wear controlling for date and avoiding problems of collinearity) as independent variables, to determine the effect of each factor whilst controlling for the other.

The volume of major/female brood cells was positively related to the weight of the female bee and negatively related to date, whereas there was no significant relationship between residual wing condition and brood cell volume (Table 2). The volume of the minor brood cells was also positively related to female weight but there was no change in minor cell volume as the season progressed and no effect of female wing condition (Table 2).

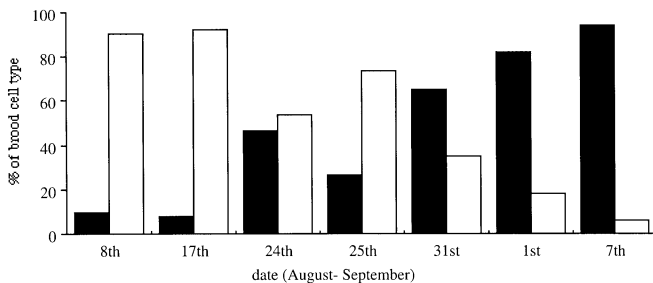
The effects of female weight and date on the probability of a female producing a major/female or a minor offspring were analysed simultaneously using a logistic regression. There was a positive effect of female weight on the probability of a nesting female producing a major/female (likelihood-ratio  $\chi^2=6.19$ ,  $P=0.011$ ; Fig. 6A), and there was a highly significant negative effect of date on the probability of producing a major/female (likelihood-ratio  $\chi^2=69.4$ ,  $P<0.0001$ ; Fig. 6B). In other words, larger females were more likely to produce major/female off-

**Table 2** Multiple regression of female weight, date and female residual wing condition on major male/female and minor male brood cell volumes. These tests and the logistic regressions performed on the same data are robust to Bonferroni correction

Source	Coefficient	df	MS	F	P
Major male/female brood cells					
Model	2.313±0.257	3	0.66	8.419	0.0001
Residual wing condition	-0.006±0.017	1	0.009	0.121	0.730
Date	-0.011±0.003	1	1.126	14.321	0.0002
Female weight	0.013±0.004	1	0.736	9.36	0.0026
Error		152	0.078		
Minor brood cells					
Model	1.280±0.271	3	0.0936	2.86	0.04
Residual wing condition	-0.014±0.028	1	0.008	0.24	0.626
Date	-0.003±0.002	1	0.064	1.94	0.168
Female weight	0.011±0.004	1	0.201	6.15	0.016
Error		55	0.033		



**Fig. 6** Logistic regressions of female weight (A) and date in the nesting season (B) on the probability of a female provisioning a major/female offspring. Figures are drawn by cubic splines FORTRAN 77 (Schlutter 1988). The *centre line* represents the mean of 1,000 bootstrap iterations, the *higher and lower lines* are the most extreme lines produced by the bootstrap



**Fig. 7** Changes in the proportions of the two size classes of plaster cast brood cells excavated over the season (*solid bars* % small cells for minor males, *open bars* % large cells for majors and females)

spring, and females nesting later in the season were more likely to produce minors.

The distribution of prepupal weights was distinctly bimodal with no overlap in weight between the two distributions (minor mean=0.604±0.005 g and range 0.4–0.8,  $n=163$ ; major/female mean=1.25±0.118 g and range 0.98–1.61,  $n=137$ ). Figure 7 shows the proportion of small (minors) to large (major/female) brood cell types on sampling dates throughout the season. Females produced fewer and fewer large brood cells and more and more small ones over time.

In the course of excavating plastered terminal brood cells, other cells associated with the plastered burrow tunnels were uncovered. The excavation of these cells revealed that some females placed one brood cell directly over the cap of a lower cell. When females stacked one brood cell on top of the other, they produced a major/female in the lower cell and a minor in the upper cell [minor (S) over major/female (L)=10, L over L=3, L over S=0, S over S=3;  $\chi^2$  (Yates corrected)=10.68,  $df=3$ ,  $P=0.025$ ].

## Discussion

### The production of minors: the mixed-ESS hypothesis

We return now to the central question, why do female Dawson's burrowing bees produce so many minors, when small sons provide such low fitness pay-offs compared to major males? As noted before, the provisioning behaviour of *A. dawsoni* could be an example of a mixed ESS in which the female bee gains equal reproductive pay-offs from producing fixed ratios of large and small male offspring, as has been suggested for several hymenopterans (Alcock et al. 1977; Alcock 1996a; Torchio and Tepedino 1980). The mixed-ESS hypothesis predicts that females of Dawson's burrowing bee should continue their production of major and minor offspring in a fixed ratio regardless of any experimental manipulations of their condition. In fact, as predicted, females that had been handicapped by weights or wing clipping did not differ in the proportion of minor males produced from untreated females.

However, to conclude that a mixed ESS applies to this case may be premature. First, the failure of the bees to produce minors may have stemmed from a failure of our experiments to produce sufficiently large foraging handicaps for the experimental females. Indeed, our manipulations did not reduce the amount of time that bees spent on their foraging trips; moreover, only the wing-clipped females reduced the weight of the provisioning loads carried back to the nest per trip.

In honey-bees, similar attempts to perturb the foraging tactics of females have also yielded equivocal results. In one study, permanent weights reduced the number of flowers visited and caused bees to return to the hive with less nectar, compensating for the added weight (Schmid-Hempel 1986). However, a later study found that weights of up to 80% of the bee's weight did not cause bees to compensate by returning with less nectar. Moreover, there were also no differences in the trip times or the frequency of trips (Wolf and Schmid-Hempel 1989). The failure of extreme loading of honey-bees to affect foraging is consistent with the negligible results of our less severe loading manipulations of nesting Dawson's burrowing bees.

Likewise, although the removal of the forewing margin of the bumble-bee, *Bombus melanopygus*, reduced the longevity of the bees, there was no effect on the duration of foraging trips or the pollen load of the returning bees (Cartar 1992). In our experiment, the wing-clipping treatment did appear to stress the bees since they carried lighter provisioning loads back to the nest, and yet this effect did not cause the bees to produce a greater proportion of less costly minors.

Second, our manipulations may have had no effect on provisioning tactics because the experiments were done early in the season at a time when the bees had access to abundant food resources. At this time, unmanipulated females were producing large offspring almost to the complete exclusion of minors (Figure 7). During this stage of the flight season, the experimental females may have also based their provisioning decisions directly on their experiences with the flowering plants rather than on their body condition. If so, the cues of food abundance may have overridden any effects of wing clipping or the added weight.

The production of minors:  
the conditional-strategy hypothesis

If females do make conditional decisions about the allocation of brood provisions in accordance with their experience with the food resource itself, then they should be more likely to produce minor males when pollen and nectar are less available. Over the flight season, we documented a decrease in the abundance of flowers that were open and the number of flower buds yet to open. As flower abundance declined, foraging times increased, presumably because females attempted to collect the same weight of pollen and nectar per trip throughout

their lifetime. Because provisioning loads remained the same throughout the season even as resources became more scarce, the foraging costs to females in terms of flight time and energy expended per trip clearly increased.

In many bees and wasps, a scarcity of food correlates with a switch to the production of the cheaper sex (e.g. Torchio and Tepedino 1980; Strohm and Linsenmair 1997; Kim 1999). As predicted from the conditional-strategy hypothesis, female Dawson's burrowing bees also became much more likely to provision for minor sons as the season progressed and foraging resources became scarce. One could argue, however, that the increased probability of producing a minor as the season drew to a close was due not to a conditionally mediated switch but rather to a fixed strategy in which female offspring were produced first and male offspring second (Torchio and Tepedino 1980; Frohlich and Tepidino 1986). Our data, however, show that nesting females produce minors almost exclusively at the end of the season and do not follow the optimal ESS ratio of two minors to one major (based on an average time cost of producing two minors for one major). This result suggests a conditionally mediated switch towards minor production at the end of the season when resources are scarce.

Some studies have documented changes in female provisioning patterns over time even where pollen and nectar were available ad libitum (Frohlich and Tepidino 1986). These patterns suggest that either females are less efficient with time (Torchio and Tepedino 1980) or that the probability of dying influences provisioning decisions (Frohlich and Tepidino 1986). In Dawson's burrowing bee, however, wing wear, which increased over the flight season and could have contributed to the conditional tendency to produce minors, actually seems to have had little effect. In contrast, female mass seems to have greatly influenced provisioning tactics, as expected from the conditional-strategy hypothesis. Large females tended to produce large brood cells for large offspring whereas small females tended to provision small brood cells designed for minor sons. Here too the conditional effect may be related to time costs for the collection of resources. We found that small females carry lighter provisioning loads than large ones, which means that smaller females must make more trips than large competitors in order to fill a brood cell of a given size. Under these circumstances, small bees may be forced to make the best of a bad job, which is to provision minor cells sooner than larger female bees do.

A further impetus for smaller females to produce minor sons lies in their apparent inability to build relatively large brood cells in the large male/female size class. If small females can only produce rather small major sons, they may receive little pay-off from a costly major, given that smaller majors are less likely to mate because of intense competition from larger majors.

## Unresolved issues

The ability of female Hymenoptera to control the sex and size of their progeny creates a situation that would seem to favour the spread of a mixed ESS (Alcock 1996b). However, the scarcity of clear examples of mixed ESSs probably arises because of the fitness advantage gained by individuals that can adaptively alter fixed decision rules (Gross 1996). Although the data on Dawson's burrowing bees offer clear evidence for the existence of such a flexible provisioning strategy, the conditional strategy is possibly superimposed on a mixed ESS. A similar pattern has been reported for Barrow's goldeneye duck, *Bucephala islandica*, in which a mixed female nest parasitism strategy becomes conditional at high population densities (Eadie and Fryxell 1992).

One special feature of the provisioning behaviour of Dawson's burrowing bee suggests a mixed ESS. During the middle to latter part of the flight season, as the bees gradually extend the more or less horizontal main nest tunnel, they sometimes build two pots, one above the other, in the brood chambers that drop down from the main tunnel. When a female stacks two brood cells together, a minor male is almost always placed above a major male or female. When this pattern is repeated, as it sometimes is, provisioning females produce large and small progeny in alternation.

This pattern makes adaptive sense because minor males emerge earlier in the season than larger bees, and their superior position ensures that they will not dig through a cell containing a larger sib on the way to the surface. As they excavate an exit tunnel, minor sons may also facilitate an easier passage through the extremely hard soil for their larger siblings, which are more reproductively valuable to their mother. Stacked cells may also provide some time and energetic savings for females in the latter part of the nesting season.

From the perspective of a mixed ESS, the alternating production of small and large brood cells demonstrates that some females can make both large and small offspring for a considerable part of the season. The precise alternation of large offspring with small offspring is suggestive of a mixed ESS operating in concert with changes in resource availability. A similar phenomena has been reported for the megachilid bee *Osmia lignaria propinqua*, in which nesting females produce large female offspring early in the season and the smaller males later, in accordance with declines in resource abundance (Torchio and Tepedino 1980). Despite these temporal shifts which might be interpreted as a conditional strategy for the production of the two sexes, the investment in both was equal, suggesting that the bees were operating under a mixed ESS.

Unfortunately, in the case of Dawson's burrowing bees, we do not know if the large offspring produced late in the season are males or females because we were unable to sex prepupae. If, early in the season, nesting bees produce females and majors but then switch to females and minors late in the season, the production of males

could be said to be simply under the control of a conditional strategy. This is a reasonable scenario because females nesting late in the season tend to produce smaller large brood cells, which are likely to be designed for females, not major males, since (as noted) small major sons have particularly low reproductive success but high costs. If, however, females produce major and minor sons in the same period, this result would suggest a complex female provisioning strategy with elements of both a mixed ESS and a conditional strategy. This possibility is, however, undercut by the evidence that provisioning females at the very end of the season are almost certainly producing minors to the near exclusion of all other offspring.

In conclusion, the evidence for the conditional production of minor males dependent on female size is compelling, whilst the seasonal increase in minor production also provides strong evidence for a conditional response to declining resources. These two conditional features of the production of minor males go a long way to explain their abundance. However, a complete understanding of why nesting females produce so many minor sons of such low reproductive value will require a technique to sex the prepupal offspring of Dawson's burrowing bee.

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