

## Brood care by male bumble bees

(thermoregulation/male behavior/kin selection/parental manipulation)

SYDNEY A. CAMERON

Department of Entomology, University of Kansas, Lawrence, KS 66045

Communicated by Charles D. Michener, June 13, 1985

**ABSTRACT** Male *Bombus griseocollis* (Hymenoptera: Apidae) share in the brood care of nestmates by incubating pupae (usually during the first few days after they emerge as adults). Male posture during incubation of a pupa is identical to that observed for females. Pupae incubated by males were 4°C–6°C above the temperature of unincubated pupae. Although this increase was not as great as that caused by workers or queens, it was an important factor in warming pupae. Incubating males may benefit nestmates incidentally without lowering their own individual fitness.

Although temperature regulation of offspring by solitary insects is not common, it is common among social insects within the nest. In Hymenoptera, this and other cooperative activities involve primarily females (the workers are females). Genetic reasons for expecting nestmate cooperation among females but not among males in haplodiploid organisms have been widely accepted (1). Nonetheless, references to work performed by males appear occasionally in the literature. In this study, I report that male bumble bees (*Bombus griseocollis*) play a significant role in incubating pupae.

### MATERIALS AND METHODS

A laboratory colony of *B. griseocollis* containing a healthy egg-laying queen (reproductive female), three broods of workers (nonreproductive female offspring,  $n = 30$ ), and males ( $n = 15$ ) was studied in July 1982. The nest was in a 33.5 × 23.0 × 24.5 cm clear Plexiglas box maintained in darkness except when observations were being made. No insulation material was provided. Honey and pollen from *Apis* hives were provided ad libitum. To facilitate observations and increase the temperature-control activity, all but 10 adults were removed from the nest an hour before observations; those remaining included the queen and 9 of her offspring, 2 incubating workers, and 7 randomly selected males. Thus, during an experiment, the worker population was smaller than usual for a colony at the male-producing stage. The previously removed colony adults were returned to the nest after each experiment. The brood consisted of 15 pupae. Incubation temperatures of pupae within cocoons were measured with thermocouples at 48-sec intervals. Four thermocouples were used: two were placed inside separate cocoons to record temperatures in the air spaces along the sides of the pupae [ $t_{C(1)}$  and  $t_{C(2)}$ ]. The apertures in the cocoons for the thermocouples were sealed with stopcock grease, which had no apparent effect on the bees. The third thermocouple was suspended inside the nest box ≈10 cm above the cells to measure the internal ambient temperature [ $t_{A(int)}$ ], and the fourth thermocouple measured the ambient temperature outside the nestbox [ $t_{A(ext)}$ ]. Pupal temperatures were recorded under a variety of external ambient temper-

atures including 21°C–24°C, 17°C, and 7°C. During temperature recording, incubation activity by a male, worker, or queen was noted for each cocoon incubated. At  $t_{A(ext)}$  of 7°C, 1–3 males tended to cluster on cocoons. Abdominal surface temperatures of males were also measured, with thermocouples placed on their dorsa.

### RESULTS

*B. griseocollis* males assume the same characteristic incubation posture on the cocoons as do the females (Fig. 1). An incubating bee extends its legs around the cocoon and elongates its abdomen, wrapping itself about the cocoon with its thorax and abdomen pressed against the cocoon. It then visibly pumps its abdomen. Heinrich (2, 3) has demonstrated that in queens of *Bombus vosnesenskii* this pumping activity regulates the flow of heat from the thorax to the abdomen to the brood.

Fig. 2 demonstrates temperature regulation of two pupae by the queen and males at room temperature [ $t_{A(ext)} = 20^\circ\text{C}$ ]. The temperature of an unattended pupa [ $t_{C(1)}$ ] was 23.5°C under external ambient temperature (20°C) at time 0. A queen raised the temperature to ≈28°C; then, 12 min after the onset of temperature recording, a single incubating male replaced the queen on  $t_{C(1)}$ . Initially, the temperature dropped, but in <1 min, the male raised the temperature to that maintained by the queen—i.e., 3°C–4°C above its unattended level. A queen (weighing approximately twice as much as the average male) joined the male during its 20-min incubation, which caused the temperature to increase ≈1.5°C. When the queen left, the male continued to incubate but  $t_{C(1)}$  dropped to 27°C. The temperature remained at this level for another 6 min. During the next 6 min, the queen replaced the male and  $t_{C(1)}$  increased to 32°C. A male then replaced the queen and maintained the temperature at ≈28°C for >30 min (including a brief period when the male was joined by the queen), until the experiment was terminated. Comparisons of simultaneous temperature recordings of unattended pupae and male-incubated pupae (Fig. 2) indicate that although the temperature of an unattended pupa remained ≈1°C above nest ambient temperature, the male-incubated pupa was maintained 4°C–6°C higher than ambient temperature. In another recording session, for each of 200 simultaneous temperature recordings of an unattended pupa and a male-incubated pupa, the temperature was 5°C–6°C higher for the male-incubated pupae.

The observations described above and in Fig. 2 show that at nest box temperatures [ $t_{A(int)}$ ] between 20°C and 22°C,  $t_{C(1)}$  is maintained at 25°C–32°C. It appears that the males do not provide enough heat to raise the temperature of a pupa above that produced by the queen, but they do provide enough heat to keep the temperature of the pupa from returning to ambient temperature after the queen departs. Males alone, without the aid or close proximity of the queen or workers, maintained pupal temperature 6°C above nest ambient temperature for at least 20 min (Fig. 2).

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

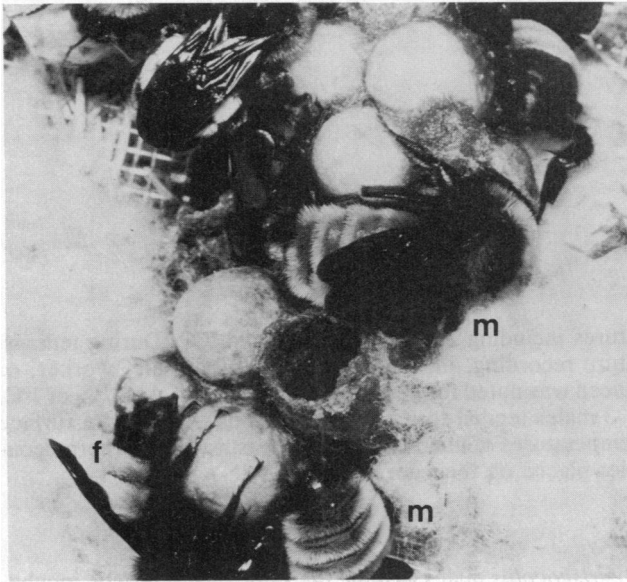


FIG. 1. Male (m) and female (f) *Bombus pennsylvanicus* incubating pupae. Both sexes assume the characteristic incubation posture with the abdomen wrapped about a cocoon.

The experiment was repeated under a much lower ambient temperature,  $t_{A(\text{ext})} = 7^\circ\text{C}$  (Fig. 3). At the start of the experiment, the nest was first placed in a warm room [ $t_{A(\text{ext})} = 25^\circ\text{C}$ ;  $t_{A(\text{int})} = 26^\circ\text{C}$ ]; the first section of Fig. 3 (0–12 min) shows the correspondingly high pupal temperatures. The nest was then placed in a cold chamber ( $7^\circ\text{C}$ ), and the pupal temperatures dropped at a slower rate than the nest box temperature,  $t_{A(\text{int})}$ , which remained well above  $t_{A(\text{ext})}$  for >40 min (Fig. 3). Males maintained  $t_{C(1)}$  near  $31^\circ\text{C}$  for 6–7 min.

The unattended pupae cooled more rapidly than male-incubated pupae. In Fig. 3,  $t_{C(1)}$  dropped  $3^\circ\text{C}$  in 1 min when the queen and a male departed. After 1 min, a male returned and the temperature then dropped more slowly ( $0.5\text{--}1.0^\circ\text{C}$  per min) for  $\approx 3$  min, at which time the pupal temperature stabilized at  $18.5^\circ\text{C}\text{--}19.0^\circ\text{C}$  for 9 min,  $12^\circ\text{C}$  above  $t_{A(\text{int})}$  and

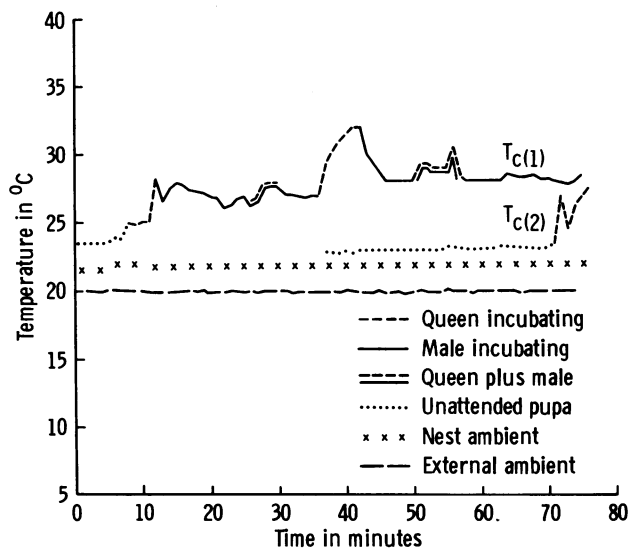


FIG. 2. Nest and pupal temperatures in a nest of *B. griseocollis* at an ambient temperature of  $20^\circ\text{C}$ . Temperatures were recorded from four thermocouples: one recorded external ambient [ $t_{A(\text{ext})}$ ]; one recorded the internal ambient of the nest [ $t_{A(\text{int})}$ ]; the others measured the temperature of two different pupae,  $t_{C(1)}$  and  $t_{C(2)}$ .

$14^\circ\text{C}$  above  $t_{A(\text{ext})}$ . Males continued to keep pupal temperatures constant even after the nest had been exposed to an external ambient temperature of  $7^\circ\text{C}$  for 40 min. At 68 min into the experiment (Fig. 3), all bees were removed from the nest; the temperatures of the two pupae decreased rapidly toward ambient temperature.

Males were not merely acting as insulation for the pupae by reducing the surface area exposed to the air; a freshly killed male wrapped around a cocoon in a manner that closely resembled a live incubating bee had no effect on pupal temperature except to cause a momentary increase of  $1^\circ\text{C}$ , probably due to heat transfer from the still warm male. In 1.5 min, the pupal temperature returned to ambient.

Do incubating males expend energy while incubating? I measured abdominal temperatures from dead males, from live but inactive males that were not incubating, and from incubating males at  $t_{A(\text{ext})} = 22^\circ\text{C}$ . Dead males had abdominal temperatures equal to ambient while inactive, live males had a mean abdominal temperature of  $24^\circ\text{C} \pm 0.36^\circ\text{C}$  ( $n = 10$ ). The incubating males, however, had a mean abdominal temperature of  $30.1^\circ\text{C} \pm 1.0^\circ\text{C}$  ( $n = 10$ ).

In addition to *B. griseocollis*, I have observed both wild and laboratory-reared colonies of *B. pennsylvanicus*, *Bombus affinis*, and *Bombus bimaculatus*. In *B. pennsylvanicus*, I obtained results similar to those reported here for *B. griseocollis*. In each species, the incubation posture of the males appeared identical to that of *B. griseocollis*. Incubation by males of various ages occurs in natural nests (unpublished observations); I have observed this behavior in most field-collected colonies. The number of older incubating males is small ( $\approx 10\%$ ), but all callow (newly emerged) males regularly incubate during their first 24–36 hr (unpublished observations).

## DISCUSSION

Male incubation behavior may be adaptive if the cost of incubation is lower than the benefit to either personal or inclusive fitness. In bumble bees, the personal cost males incur by incubating is probably often minor because (i) they cannot fly during the first 24 hr after emergence, so leaving the nest to mate would not be possible; and (ii) the potential

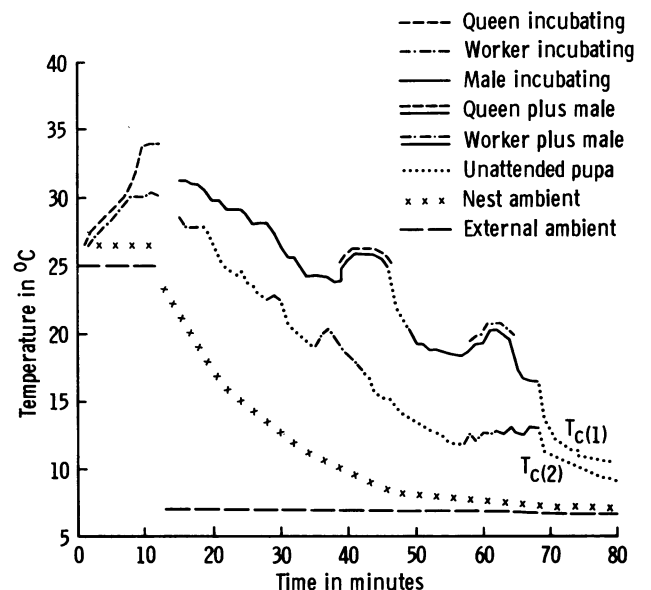


FIG. 3. Nest and pupal temperatures in a nest of *B. griseocollis* at ambient temperatures of  $25^\circ\text{C}$  and subsequently at  $7^\circ\text{C}$ . Recording conditions are the same as described in Fig. 2.

personal benefit of exercising the flight muscles during incubation could be great.

Although the individual contribution of an incubating male may be low during periods of high worker numbers, male incubation may have a large impact on brood survivorship toward the end of the colony cycle when most of the workers have died and the relative proportion of males in the colony may be higher. One field-collected colony of *B. pennsylvanicus* survived many months in the laboratory; eventually the adult population was reduced to only seven males that continued to incubate for >2 weeks. Brood continued to emerge when only males were present to incubate.

Alternatively, parental manipulation (4) could be operating; selfish selection could favor a reproductive female who manipulates her offspring so that they help her rear other offspring. We know that queens produce pheromones that suppress worker oviposition (5, 6), and these pheromones may also affect other offspring. It is conceivable that males could be similarly dominated by the queen. However, I have observed males incubating long after a queen has died (see above), so maternal control alone cannot suffice to explain male brood care.

In another eusocial hymenopteran, *Polistes major*, males may engage in brood care. Male *Polistes* (paper wasps) sometimes feed larvae with food received from returning foragers (7, 8). West-Eberhard (9) has "...seen male Hymenoptera (*Polistes*) carry out every common worker

duty except bringing prey and building material to the nest." She and I have also independently observed fanning by male *Polistes* to cool overheated nests (8, 9), an interesting contrast to the incubation behavior in *Bombus*.

I thank H. B. Lillywhite for use of his laboratory. I also thank D. B. Wahl for invaluable assistance in rearing the bumble bee colonies and A. J. Nachbaur, professional beekeeper, for supplying pollen with which they were reared. I thank C. D. Michener, H. B. Lillywhite, J. M. Hollander, J. H. Hunt, W. T. Wcislo, T. Allen, and J. B. Whitfield for critical review of the manuscript. The study was supported by the National Science Foundation (Grants BNS82-00651 and BNS82-05566; C. D. Michener, principal investigator). This is contribution 1854 from the Department of Entomology, University of Kansas, Lawrence.

1. Hamilton, W. D. (1964) *J. Theor. Biol.* **7**, 1–52.
2. Heinrich, B. (1972) *Nature (London)* **239**, 223–225.
3. Heinrich, B. (1974) *J. Comp. Physiol.* **88**, 129–140.
4. Alexander, R. D. (1974) *Ann. Rev. Ecol. Syst.* **4**, 325–383.
5. van Honk, C. G. J., Velthuis, H. H. W., Röseler, P. F. & Malotau, M. E. (1980) *Entomol. Exp. Appl.* **28**, 191–198.
6. Röseler, P. F., Röseler, I. & van Honk, C. G. J. (1981) *Experientia* **37**, 348–351.
7. Hunt, J. & Noonan, K. C. (1979) *Insectes Sociaux* **26**, 247–251.
8. Cameron, S. A. (1985) *J. Kans. Entomol. Soc.*, in press.
9. West-Eberhard, M. J. (1969) *Misc. Publ. Mus. Zool. Univ. Mich.* **140**, 1–101.