Brood care by male bumble bees

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

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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. Al-
though 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 fe-
males). Genetic reasons for expecting nestmate cooperation
among females but not among males in haplodiploid orga-
nisms have been widely accepted (1). Nonetheless, refer-
ences 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 temper-
ature 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 thermocou-
ples placed on their dorsa.

RESULTS

B. griseocollis males assume the same characteristic incuba-
tion 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 [$t_{A(ext)} = 20°C$].
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 simulta-
neous 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 pupa.

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, main-
tained pupal temperature 6°C above nest ambient tempera-
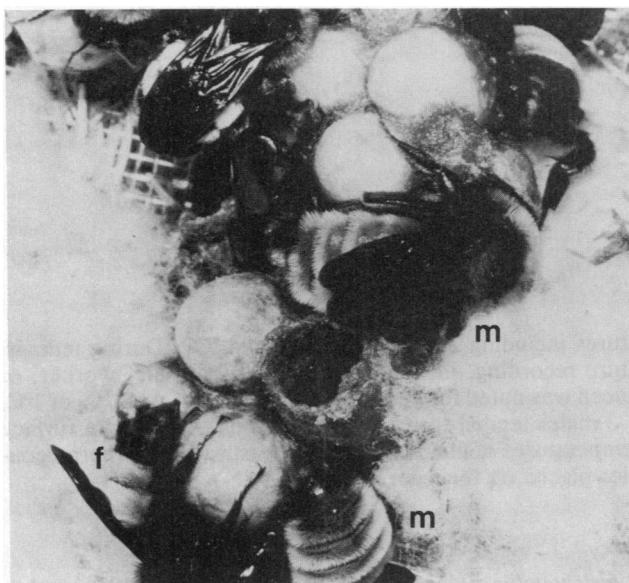ture for at least 20 min (Fig. 2).

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, $t_{A(ext)} = 7°C$ (Fig. 3). At the start of the experiment, the nest was first placed in a warm room [$t_{A(ext)} = 25°C$; $t_{A(int)} = 26°C$]; 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°C), and the pupal temperatures dropped at a slower rate than the nest box temperature, $t_{A(int)}$, which remained well above $t_{A(ext)}$ for >40 min (Fig. 3). Males maintained $t_{C(1)}$ near 31°C for 6–7 min.

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

14°C above $t_{A(ext)}$. Males continued to keep pupal temperatures constant even after the nest had been exposed to an external ambient temperature of 7°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°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 $t_{A(ext)} = 22°C$. Dead males had abdominal temperatures equal to ambient while inactive, live males had a mean abdominal temperature of 24°C ± 0.36°C ($n = 10$). The incubating males, however, had a mean abdominal temperature of 30.1°C ± 1.0°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 (≈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

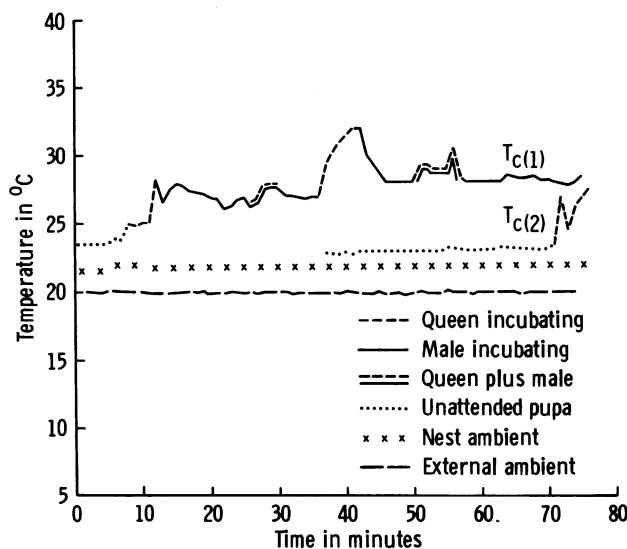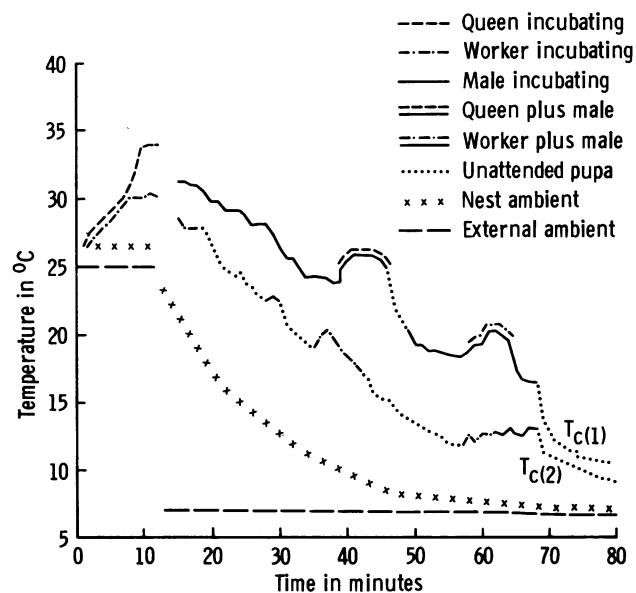
FIG. 2. Nest and pupal temperatures in a nest of *B. griseocollis* at an ambient temperature of 20°C. Temperatures were recorded from four thermocouples: one recorded external ambient [$t_{A(ext)}$]; one recorded the internal ambient of the nest [$t_{A(int)}$]; the others measured the temperature of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

FIG. 3. Nest and pupal temperatures in a nest of *B. griseocollis* at ambient temperatures of 25°C and subsequently at 7°C. Recording conditions are the same as described in Fig. 2.

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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*.

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