

Territorial behaviour in males of three North American species of bumblebees (Hymenoptera: Apidae, *Bombus*)

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The behaviour of males of the bumblebees *Bombus nevadensis nevadensis*, *B. griseocollis*, and *B. rufocinctus* was examined at sites in Colorado and Montana, U.S.A. Males of all three species defended individual mating territories on which they scent marked plants with cephalic chemicals, which we hypothesize to be sex pheromones. Males aggressively excluded conspecific males from the vicinity of scent-marked plants for several hours each day. At times on certain *B. griseocollis* territories, the great number of intruding males resulted in a near breakdown of the territorial system, with repeated aggressive interactions and turnover. In preliminary chemical analyses, dichloromethane extracts of heads of *B. nevadensis* and *B. griseocollis* were each dominated by single components, while those of *B. rufocinctus*, in each population studied, had three major components. Extracts of plant parts scent marked by males reveal the presence of the cephalic chemicals not present on unmarked control plants. Mating is initiated on or near territories. The behavioural and morphological correlates of male mating systems in the genus *Bombus* and other aculeate Hymenoptera are discussed.

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Le comportement de bourdons mâles, *Bombus nevadensis nevadensis*, *B. griseocollis* et *B. rufocinctus*, a fait l'objet d'une étude en différents endroits du Colorado et du Montana, États-Unis. Chez les trois espèces, les mâles défendaient chacun un territoire de reproduction dans lequel ils marquaient des plantes au moyen de substances chimiques céphaliques que l'on suppose être des phéromones sexuelles. Les mâles excluaient les autres mâles conspécifiques de façon agressive du voisinage des plantes marquées durant plusieurs heures chaque jour. Chez certains *B. griseocollis*, les territoires se sont avérés tellement envahis par des mâles intrus, que le système territorial a été presque aboli par des agressions répétées et par un important taux de remplacement des mâles dans les territoires. Au cours d'analyses chimiques préliminaires, nous avons constaté que les substances céphaliques extraites au dichlorométhane étaient dominées par une seule composante chez *Bombus nevadensis* et *B. griseocollis*, alors que celles de *B. rufocinctus* contenaient trois composantes principales. L'analyse de parties marquées de plantes par extraction a révélé la présence de substances chimiques céphaliques absentes des plantes témoins non marquées. Les accouplements ont lieu dans les territoires ou dans le voisinage. Les corrélations entre le comportement et la morphologie dans les systèmes d'accouplement chez les mâles du genre *Bombus* et chez d'autres Hyménoptères aculéates font l'objet d'une discussion.

[Traduit par la rédaction]

Introduction

Although bumblebees are abundant and conspicuous throughout North America, there are few published reports of male mating strategies. European workers have been more diligent in this respect, beginning with Newman (1851), Darwin (1886), and Sladen (1912), and reviewed recently by Alford (1975). In probably the majority of species, males repeatedly fly circuits along a series of widely separated sites that they scent mark with pheromones (Alford 1975; Svensson 1979; Duffield *et al.* 1984). Males are not territorial, so large numbers of males may share single flight paths (Stiles 1976). Virgin queens visit the scent-marked sites along circuits that males may maintain on consecutive days (Haas 1949; Kruger 1951; Kullenberg 1973; Kullenberg *et al.* 1973). The pheromones of nearly 20 species have been identified (Duffield *et al.* 1984; Free 1987).

In other *Bombus* species, males focus their activities around nests. In some, males fly circuits that intersect a number of nest entrances (Svensson 1980), while in others they perch at nest entrances and compete aggressively for emerging virgin queens (Frison 1930; Kruger 1951; Alford 1975; Lloyd 1981; Villalobos and Shelly 1987). Male scent marking has not been reported in any of these species.

Finally, males of other species defend small territories on

which they await females. The first record of North American *Bombus* males exhibiting territoriality was apparently that of Frison (1917), who reported drones of *B. nevadensis auricomus* (Robertson) (reported as *B. auricomus*) "hovering for hours about a particular fence-post in the sun, and from there darting out from time to time." He also reported that *B. griseocollis* (DeGeer) (reported as *B. separatus*) "has the same habit of selecting fence-posts, trees, and other prominent objects, and remaining about them for many hours." Hobbs (1965) observed this behaviour in *B. nevadensis nevadensis* Cresson in Alberta, Canada, and also reported males darting at queens, clasping them with their legs, and falling to the ground. Recently, Alcock and Alcock (1983) reported that males of *B. nevadensis auricomus* and *B. griseocollis* in Virginia apparently scent marked stems on territories and that individual males returned daily to the same perches for up to 24 days.

To date, scent-marking chemicals have not been analyzed in the territorial species. Here, along with data on territorial behaviour and spatial and temporal patterns of male activity, we present preliminary analyses of the chemicals that males of *B. nevadensis nevadensis*, *B. griseocollis*, and *B. rufocinctus* Cresson apply to plants within their territories at sites in Colorado and Montana, U.S.A.

Methods

Study areas

Studies of *B. n. nevadensis* and *B. rufocinctus* were conducted in 1986, 1987, and 1988 23 km west of Livermore, Larimer County, Colorado, at an altitude of 2250 m, in an ungrazed meadow containing scattered shrubs, chiefly snowberry (*Symphoricarpos* sp.), currant (*Ribes* sp.), skunkbrush sumac (*Rhus trilobata* Nutt. ex T. & G.), and chokecherry (*Prunus virginiana* L.), with patches of willow (*Salix* sp.) along an intermittent stream.

Bombus griseocollis and second populations of *B. rufocinctus* and *B. nevadensis* were studied July through September 1987 and 1988 at a site 9 km south of Three Forks, Gallatin County, Montana, at an altitude of 1300 m. This grassland site also contained yellow sweet clover (*Melilotus officinalis* (L.) Lam.), purple prairie clover (*Petalostemon purpureum* (Vent.) Rydb.), prairie coneflower (*Ratibida columnifera* (Nutt.) Woot. & Standl.), junipers (*Juniperus* spp.), and *Rhus trilobata*.

Behavioural observations

Territories were marked with numbered stakes, mapped, and censused on a nearly daily basis. On 12 days at the Montana site, extensive surveys were undertaken either continuously or at 30-min intervals. Males were marked with one to three dots of Testor's® coloured enamel paint on the thoracic dorsum. Observational sampling included (i) 10-min focal observational samples taken at half-hourly or hourly intervals and (ii) *ad libitum* recording of scent marking, aggressive interactions, and encounters between males and females. Means are presented \pm standard error.

Chemical analyses

Heads, thoraces, and abdomens of males were collected and immediately placed in dichloromethane (glass distilled). We also placed stems and leaves "scent marked" by males of *B. nevadensis* and *B. rufocinctus* in dichloromethane to determine if substances from males were deposited on plants. Control stems and leaves were taken from nearby plants of the same species that had not been scent marked. Males and plant parts were handled only with forceps and scissors rinsed with dichloromethane between each use.

All extracts were analysed with a Hewlett-Packard 5890 gas-liquid chromatograph (GLC), using a methyl silicone capillary GLC column (5 m \times 0.5 mm) temperature programmed from 60 to 240°C at 10°C/min with a 1-min delay, with nitrogen as a carrier gas, and with flame-ionization detection. GLC analyses were quantified with a Hewlett-Packard integrator-recorder.

Results

General description of male behaviour

Bombus nevadensis

Territorial males were present at the Colorado site from 27 through 29 July 1986 and from 27 July through 5 August 1987. During both seasons, males may have been active earlier. They were typically present on territories from 07:30 to 12:00, perched 0.4–0.8 m high atop herbs and shrubs. Each male used the same perch repeatedly, often a plant stem projecting above the surrounding vegetation. They occasionally used nearby alternative perches, but never the soil surface. Perched males held their wings slightly extended, with their antennae rigidly forward and their body frequently tilted slightly upward.

In 1986, four territories were located in the meadow at the Colorado site. In 1987, 13 territories, separated from one another by 3–54 m, were found along a little-used dirt road to the west of the 1986 site (Fig. 1A). No territories were found in 1988. Because only one territory each year from 1987 to 1989 was found at the Montana site (several hundred metres from the territories of the other two species), observations reported here are from the Colorado population.

On territories, males undertook flights of two types: (i)

patrolling flights, circular or irregular in pattern and apparently not directed at another insect, and (ii) pursuit flights, swift and direct flights directed towards passing insects. These were normally terminated without contact unless the insect was a conspecific. Males from neighbouring territories were approached closely and sometimes butted or less commonly grappled. Conspecific females were mounted in midair and forced to the ground. Thus, pursuit flights appeared to serve as a means of approaching insects closely enough to determine whether they were conspecifics. Small and low-flying insects did not elicit pursuit flights. Males often rotated rapidly in the horizontal plane on perches, particularly in response to passing insects.

Bombus griseocollis

In 1987, territories of *B. griseocollis* were present both later in the day and later in the season than those of *B. nevadensis* (Table 1). The 24 territories censused formed a dense aggregation within an area dominated by large patches of yellow sweet clover (Fig. 1B, Table 1). Like that of *B. nevadensis*, the behaviour of *B. griseocollis* centered around a limited set of perches, 0.2–0.3 m high on plants, generally prairie coneflower or yellow sweet clover. Males generally fed from flowers only before and after the daily territorial period and continued to occupy the territories after the plants had ceased blooming.

From their perches, males pursued large passing insects for distances of up to about 20 m and engaged in intense and prolonged contests that commonly resulted in usurpation. In a typical interaction, two to five males flew together in broad looping patterns, often rising to heights of 4–5 m. Butting and grappling among males were also observed. Where territories were closely packed (e.g., around territory 7, Fig. 1B), we sometimes observed nearly constant fighting over a period of several hours.

Bombus rufocinctus

In 1987, aggregated territories of this species were interspersed with those of *B. nevadensis* in Colorado (Fig. 1A) and *B. griseocollis* in Montana (Fig. 1B, Table 1). Seasonal activity of the sympatric species also overlapped (Table 1).

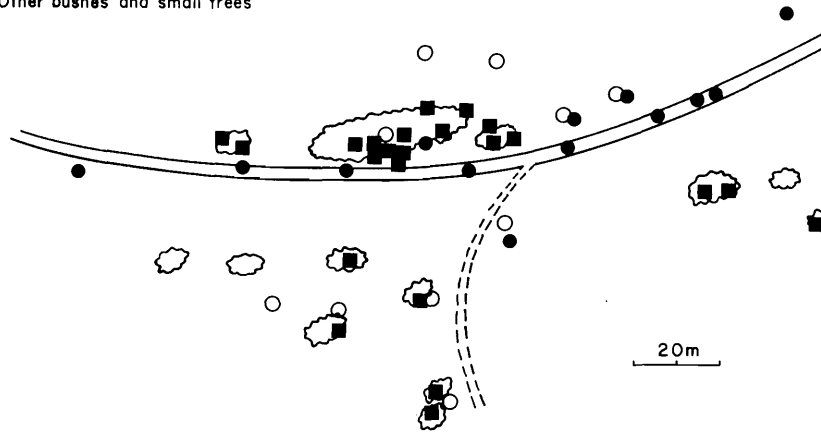
At the Colorado site in 1987, we marked 23 territories (Fig. 1A), although there were others elsewhere in the meadow. Most territories were within large clumps of *Symphoricarpos* (up to 14/patch), with broad intervening areas with no territories (Fig. 1A). In late July and early August, the *Symphoricarpos* was in bloom and attracting many bees, although no *B. rufocinctus* females were identified. Males continued to maintain territories on these plants in the later part of the summer when few or no blossoms remained. In 1988, the same bushes and territories were occupied by a similar number of males. That year males also occupied territories on *Rhus trilobata* bushes, among tall grasses.

At the Montana site in 1987, the area containing *B. griseocollis* territories also included territories of *B. rufocinctus* (Fig. 1). However, many *B. rufocinctus* territories were also located to the west within other areas of sweet clover and to the north and northeast on juniper and *R. trilobata*.

At both sites, the behaviour of male *B. rufocinctus* resembled that of *B. nevadensis* and *B. griseocollis*. The posture on the perches was similar, but the longer antennae of *B. rufocinctus* males were invariably twisted to the side apically. Unlike *B. nevadensis* and *B. griseocollis*, *B. rufocinctus* frequently changed perches and used perches varying in height from the soil surface to over 3 m on willow and junipers. Because several

(A) COLORADO SITE

- *Bombus rufocinctus* territory
- *Bombus nevadensis* territory
- ☁ *Symphoricarpos* patches
- Other bushes and small trees



(B) MONTANA SITE

- *Bombus rufocinctus* territory
- *Bombus griseocollis* territory
- Scent-marked stems (*B. griseocollis*)
- ★ *Bombus griseocollis* nest entrance

- ☁ Patches of yellow sweet clover
- ⋯ Patch of purple prairie clover

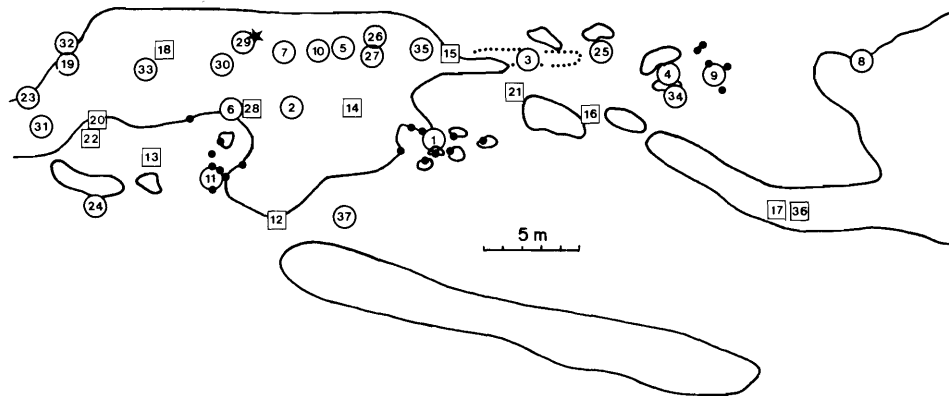


FIG. 1. Maps of the study sites in (A) Colorado and (B) Montana, showing position of territories.

territories were often packed into a patch of *Symphoricarpos*, a great many pursuit flights were directed towards neighbouring males, as well as other large flying insects and birds. Contests rarely involved butting or grappling. Although the aggregations of *B. rufocinctus* overlapped with both *B. nevadensis* and *B. griseocollis*, we did not observe aggression among the species.

Scent-marking behaviour

In all three species, territorial males flew to plants near their perches and walked slowly up the stem over a distance of 5–40 cm. The head, thorax, and abdomen were held close to the stem, which was grasped tightly with all six legs; the wings were spread slightly and sometimes beat rapidly. On leaves of *Rhus*, *B. rufocinctus* went along the margins of leaves, covering up to 10 leaves in a single bout of scent marking.

The locations of the plants scent marked by male *B. griseocollis* on territories 1, 9, and 11 (observed 1 day each) are shown in Fig. 1B. The stems were an average distance of 1.3 ± 0.2 (SE) m from their perches ($N = 21$). Because of this and the close packing of territories in some places, scent-marked areas of this species were sometimes contiguous or even overlapping.

Dichloromethane extracts of heads of *B. griseocollis* and *B. nevadensis* were dominated by single components of similar molecular weights in the two species (Figs. 2A and 2B). These components were not detected in combined thorax/abdomen extracts of *B. griseocollis* or in separate thorax and abdomen extracts of *B. nevadensis*. Extracts of plant stems from territories of *B. nevadensis*, however, show that males deposit the cephalic chemicals on stems (Fig. 3A vs. Fig. 3B). The chemical was absent from control plant extracts (Fig. 3C vs. Fig. 3D).

TABLE 1. Activity and residency patterns of male *Bombus*; ranges of nearest-neighbor distances are for peak daily activity periods during the days on which the most extensive censuses were made

| | <i>B. nevadensis</i> | <i>B. griseocollis</i> | <i>B. rufocinctus</i> | |
|--|----------------------|------------------------|-----------------------|----------------------|
| | | | Colorado | Montana |
| Seasonal activity period ^a | 7/27–8/5 | 8/11–9/15 | 7/29–9/12 | 8/11–9/14 |
| Daily activity period | 07:30–12:00 | 10:00–15:00 | 08:30–11:00 | 10:00–15:00 |
| No. of territories censused | 10 | 24 | 9 | 19 |
| No. of days censused | 8 | 19 | 12 | 17 |
| No. of territories/day | 1–9 | 2–14 | 6–10 | 1–10 |
| Nearest-neighbour distances, range (N) | 3–54 (49) | 1.0–6.0 (115) | — | 0.5–11.5 (82) |
| No. of males marked | 9 | 34 | 11 | 23 |
| Mean (\pm SE) no. of different males/territory over season (range) | 1.3 \pm 0.2 (1–2) | 4.0 \pm 0.8 (1–15) | 1.6 \pm 0.2 (1–3) | 2.3 \pm 0.4 (1–5) |
| No. of different territories/ marked male, range | 1–2 | 1–6 | 1–2 | 1–2 |
| Mean (\pm SE) no. of days individual marked males territorial over season (range) | 5.2 \pm 0.5 (1–7) | 4.2 \pm 0.6 (1–14) | 6.7 \pm 1.4 (1–12) | 3.6 \pm 0.7 (1–12) |
| Maximum period individual marked male present at site (days) | 10 | 26 | 15 | 19 |

^aMonth/day.

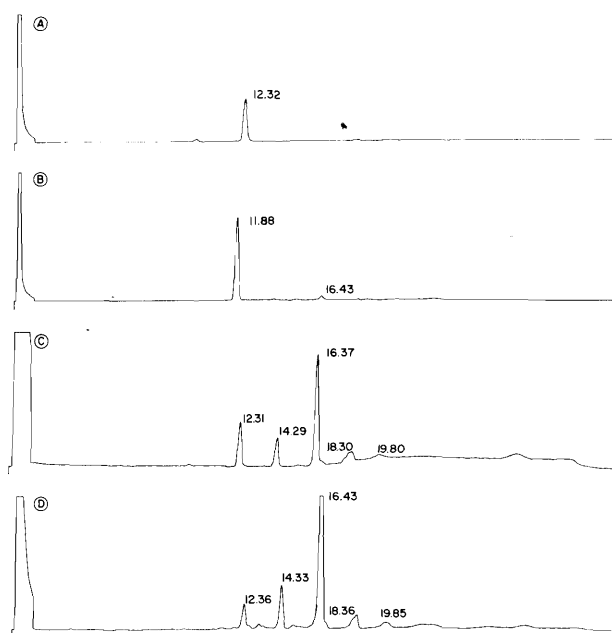


FIG. 2. Gas chromatograms of extracts in dichloromethane of heads of (A) *Bombus nevadensis*, (B) *B. griseocollis*, and (C) *B. rufocinctus* from the Colorado site, and (D) *B. rufocinctus* from the Montana site. Numbers at peaks represent GLC retention times in minutes.

Extracts of male *B. rufocinctus* heads from both sites reveal similar mixtures of three components (Figs. 2C and 2D), not present in extracts of thoraces and abdomens. The chemicals are of equal or slightly greater molecular weights than those in the *B. griseocollis* and *B. nevadensis* extracts. Although there were great numbers of chemicals present even in the control extracts of plants, GLC analysis of the plant extracts suggests that at least two, and possibly three, cephalic chemicals were deposited on the plants (Figs. 4B and 4D).

For males on which focal observations were conducted, the rate of scent marking was highest early in the day soon after the males arrived on territories (Table 2). Where sufficient numbers of samples of behaviour were available (i.e., *B. rufocinctus* at

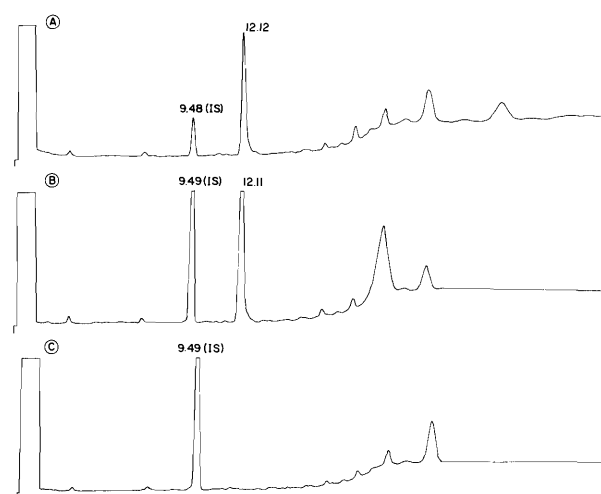


FIG. 3. Gas chromatograms of extracts in dichloromethane of (A) heads of *Bombus nevadensis*, (B) grass stems marked by males, and (C) grass stems not scent marked by males. Numbers at peaks represent retention times in minutes. IS, internal standard (hexadecane).

the Colorado site), the difference was significant (Table 2). This conclusion is substantiated by observations of scent marking during censuses of territory occupants on 3 days at the Montana site. For *B. griseocollis*, all 16 observations of scent marking occurred during the first census on which the male was present on the territory (χ^2 goodness of fit, $\chi^2_1 = 16.0$, $P < 0.001$). During censuses of *B. rufocinctus*, 21 of 22 scent marks occurred in the first 45 min of activity although males were present on territories for three further hours each day (χ^2 goodness of fit, $\chi^2_1 = 18.2$, $P < 0.001$).

Male–female interactions

Bombus nevadensis

A complete mating was observed on 30 July 1987. At 10:42, a marked, territorial male pursued and struck a female in flight. The pair landed in tall grass 10 m away, where they remained in contact for 9 min and 40 s, although not always in genital contact. The males' hind legs were held loosely at the side and

TABLE 2. Rates of scent marking during focal observation of territorial males

| | <i>B. nevadensis</i> | <i>B. griseocollis</i> | <i>B. rufocinctus</i> |
|--|----------------------|------------------------|-----------------------|
| Scent marks in first 10-min sample | | | |
| Mean | 51.0 | 7.5 | 37.3 ^a |
| SE | 3.0 | 1.5 | 5.0 |
| No. of samples | 2 | 2 | 9 |
| No. of males | 2 | 2 | 9 |
| Scent marks in subsequent samples | | | |
| Mean | 2.3 | 0.2 | 5.0 |
| SE | 1.0 | 0.2 | 1.6 |
| No. of samples | 11 | 9 | 24 |
| No. of males | 11 | 9 | 24 |
| % subsequent samples greater than first sample for each male | | | |
| | 0 | 0 | 0 |

^aMeans for this species were significantly different; *t*-test, $t_{31} = 4.86$, $P < 0.001$. Other species were not tested owing to small sample sizes (see text).

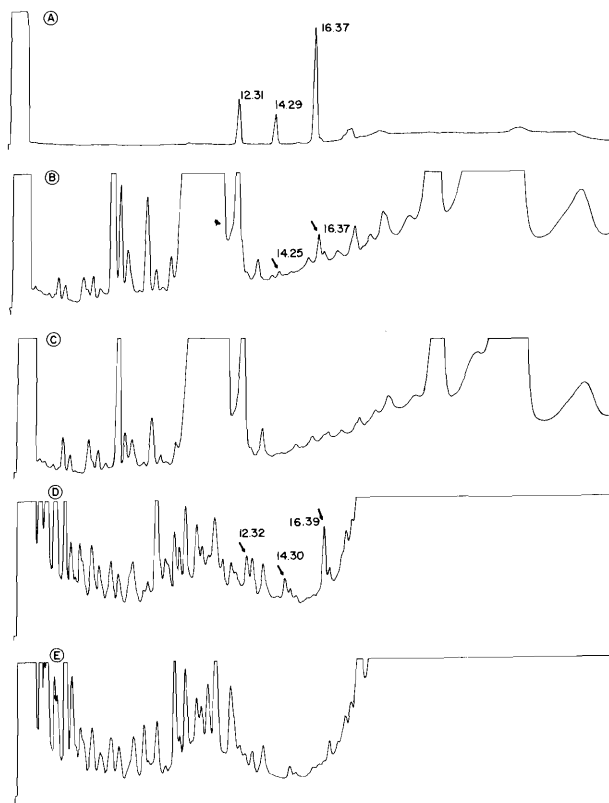


FIG. 4. Gas chromatograms of extracts in dichloromethane of (A) heads of *B. rufocinctus*, (B) *Symphoricarpos* leaves marked by males and (C) not scent marked by males (Colorado site) and (D) *Ribes* leaves marked by males and (E) not scent marked by males (Colorado site). Numbers at peaks represent retention times in minutes. Arrows indicate peaks from plant extracts thought to represent chemicals deposited on leaves by males.

during periodic genital contact and were used to stroke the posterior part of the female's abdomen rhythmically. The male eventually broke contact and the female flew off shortly thereafter. In observations of two other encounters, copulation may have occurred, but we were unable to observe the complete interactions.

Bombus griseocollis

We observed 37 prolonged interactions between males and females. These typically involved males chasing females flying

Bombus nevadensis

| TERRITORY | JULY | | | | | AUGUST | | | | |
|-----------|------|-----------------|----|----|----|--------|----|----|----------------|---|
| | 27 | 28 ^a | 29 | 30 | 31 | 1 | 2 | 3 | 4 ^a | 5 |
| | 1 | Y | | Y | Y | Y | Y | - | - | - |
| 2 | R | | R | R | G | G | G | - | - | - |
| 3 | U | | OW | OW | OW | OW | OW | OW | OW | - |
| 4 | U | | RW | RW | RW | RW | RW | RW | RW | - |
| 5 | - | | O | O | R | R | R | R | R | - |
| 6 | - | | G | G | - | - | - | - | - | - |
| 7 | - | | W | W | - | - | - | - | - | - |
| 8 | - | | YG | YG | YG | - | - | Y | - | - |
| 9 | - | | - | B | B | B | B | B | B | B |
| 13 | - | | - | - | O | O | O | O | O | - |

FIG. 5. Seasonal patterns of territory occupation by marked and unmarked males (U) of *Bombus nevadensis*. Other letters refer to colour codes used for marked males. ^aRainy days on which no territories were occupied.

to and from the *B. griseocollis* nest near territory 29 (Fig. 1B). Fifty-four percent involved multiple males (mean = 1.7 ± 0.15 , range = 1–5), including territory residents and males not residing on territories at the time.

One complete copulation was observed. After the male resident on territory 6 pounced upon a flying female, they dropped to the ground. When the female again took flight, the male again landed upon her. When they landed for a second time, 10 m away, they were coupled and the male had released his leg grasp and flipped backwards, maintaining only genital contact. They remained coupled for 12 min and 5 s before the male initiated decoupling and returned to his territory.

No other successful copulations were observed in the 22 other observations of males mounting females. Females often eluded pursuing males by landing and walking away through vegeta-

TABLE 3. The frequency of within-day changes in territory resident in three species of *Bombus*

| Species | No. of territories | Cumulative days occupied | No. of within-day changes of resident ^a | No./day per territory |
|----------------------------------|--------------------|--------------------------|--|-----------------------|
| <i>B. nevadensis</i> | 10 | 47 | 3 | 0.06 |
| <i>B. griseocollis</i> | 20 | 115 ^b | 69 | 0.60 |
| <i>B. rufocinctus</i> (Colorado) | 9 | 76 | 0 | 0 |
| <i>B. rufocinctus</i> (Montana) | 12 | 82 ^b | 11 | 0.13 |

^a χ^2 goodness of fit, $\chi^2 = 83.21$, 3 df, $P < 0.001$. Expected values are based on the null hypothesis that distribution (among species) of observations of within-day changes is proportional to the number of days territories were occupied, summed across all territories (i.e., value in column 2).

^bData from 12 extensive census days.

tion. However, because the female often carried the male in flight until they were lost from sight, further mating may have resulted.

Bombus rufocinctus

We saw no interactions between males and females at either site. In fact, queens and workers were very scarce despite the abundance of males.

Patterns of territory residency

Changes in territory ownership were infrequent in our observations of *B. nevadensis* and *B. rufocinctus* both within (Table 3) and between days (Figs. 5 and 6). Individual territories of these two species never had more than five different residents during the course of the 1987 season (Figs. 5 and 6, Table 1). Patterns of occupation of *B. rufocinctus* (Montana site) on a typical day at the height of seasonal activity are shown in Fig. 7A.

Eight of 20 *B. griseocollis* territories had just one ($N = 6$) or two ($N = 2$) residents during the course of the 1987 observations. However, others exhibited a constantly changing pattern of ownership within and between days (Table 3, Fig. 7B). Individual territories of *B. griseocollis* had up to 15 different resident males during the course of the season (Table 1) and as many as 7 on a single day. The changing ownership that resulted from fighting is especially evident on territories 7 and 29 (Fig. 7B). Forty-nine percent ($N = 69$) of the ownership changes in *B. griseocollis* were known to be immediately preceded by fights between the resident male and an intruder. Others occurred after males departed from territories in pursuit of passing females. However, males also changed territories for no obvious reason. For example, the male marked yellow (Y) moved between territories 1 and 5 and occasionally occupied no territory (Figs. 1B and 7B).

Histories of individual males

In all three species, individually marked males were seen repeatedly as residents over the course of the 1987 season (Table 1) and often maintained sole occupancy of territories for prolonged periods (Figs. 5 and 6). This was even observed in *B. griseocollis*, where three males were sole occupants on territories 1, 4, and 11 for 6–7 days.

Discussion

Male *Bombus rufocinctus*, *B. nevadensis nevadensis*, and *B. griseocollis* at sites in Montana and Colorado deposited cephalic chemicals on plants around which they aggressively excluded conspecific males for several hours each day. The areas that males occupy conform to the definition of "territory" that we have adopted in our previous studies of territorial

behaviour in male Hymenoptera (e.g., Evans and O'Neill 1988): "a fixed area from which intruders are excluded by some combination of advertisement, threat, and attack" (Brown 1975). However, at times on certain *B. griseocollis* territories, the great number of intruding males resulted in a near breakdown of the territorial system, with repeated aggressive interactions and usurpation. This may have been caused by the high density of territories and great numbers of nonterritorial *B. griseocollis* males at the site. In other insects territorial systems may break down completely at high densities (e.g., Alcock and O'Neill 1986).

In *B. nevadensis* and *B. griseocollis*, contacts with queens were initiated on or near territories. We never observed mating in *B. rufocinctus* and, in fact, rarely saw females. However, it seems safe to conclude that defended areas function as mating territories in *Bombus*, even though matings are rarely observed (see also Alcock and Alcock 1983). It is possible that the paucity of observed matings in all three species in our study was a function of the male-biased sex ratios that are common in *Bombus* (Owen *et al.* 1980; Duchateau and Velthuis 1988)).

Like other Hymenoptera, the male *Bombus* may be defending symbolic territories attractive to females solely because of the presence of males and the chemicals that they deposit (Evans and O'Neill 1988). It seems likely that *Bombus* males defend neither flower resources critical to females nor nests. Although the territories sometimes occurred on flowering plants, many did not, especially late in the season. Furthermore, large numbers of flowering plants were not defended by males. The *B. griseocollis* territories were near an active nest and males interacted repeatedly with gynes from the nest. However, this was apparently not the case in the populations of *B. griseocollis* studied by Alcock and Alcock (1983).

The overall behaviour patterns of the three species were similar in many respects. It is difficult to draw conclusions concerning differences among species in a study of this type, because the observations were made over a limited time span on just one or two populations per species. Some of the differences are seemingly trivial (e.g., apical twisting of the antennae in perched *B. rufocinctus*) or at least obscure in their evolutionary significance (e.g., perching on the soil versus perching on plant stems). While other differences are more interesting from an ecological viewpoint, it is possible that they are only apparent species differences arising from variation in sampling intensity among species (e.g., number of territories per male per season) or that they are peculiar to a particular site and year (e.g., type of vegetation in which territories occur).

One consistent difference among the species may be the spacing of territories. In the Virginia (Alcock and Alcock

(A) *Bombus rufocinctus* - Montana site

| | | AUGUST | | | | | | | | | | | | | | | | | | | |
|-----------|----|--------|----|----|-----------------|-----------------|----|----|----|----|----|-----------------|-----------------|-----------------|-----------------|----|----|----|----|-----------------|----|
| | | 12 | 13 | 14 | 15 ^a | 16 ^a | 17 | 18 | 19 | 20 | 21 | 22 ^b | 23 ^b | 24 ^b | 25 ^b | 26 | 27 | 28 | 29 | 30 ^a | 31 |
| TERRITORY | 12 | U | U | W | | | W | W | W | W | W | | | | | W | W | W | W | | W |
| | 13 | U | WW | WW | | | WW | - | - | - | - | | | | | - | - | - | - | | - |
| | 14 | U | U | W | | | | | | | | | | | | Y | Y | | | | |
| | 15 | U | W | W | | | W | W | W | W | W | | | | | W | W | W | W | | W |
| | 16 | - | U | O | | | WB | WB | WB | WB | WB | | | | | Y | Y | U | V | | V |
| | 17 | - | - | WW | | | G | | U | U | U | | | | | G | G | | | | |
| | 18 | - | - | U | | | U | WB | B | B | B | | | | | B | B | B | B | | B |
| | 20 | - | - | - | | | W | W | | U | | | | | | - | - | - | - | | - |
| | 21 | - | - | - | | | BW | | | | | | | | | - | - | - | - | | - |
| | 22 | - | - | - | | | B | | U | | | | | | | - | - | - | - | | - |
| | 28 | U | U | U | | | U | O | O | O | O | | | | | - | - | - | - | | - |
| | 29 | - | - | - | | | - | - | - | - | - | | | | | GY | GY | GY | GY | | GY |

(B) *Bombus rufocinctus* - Colorado site

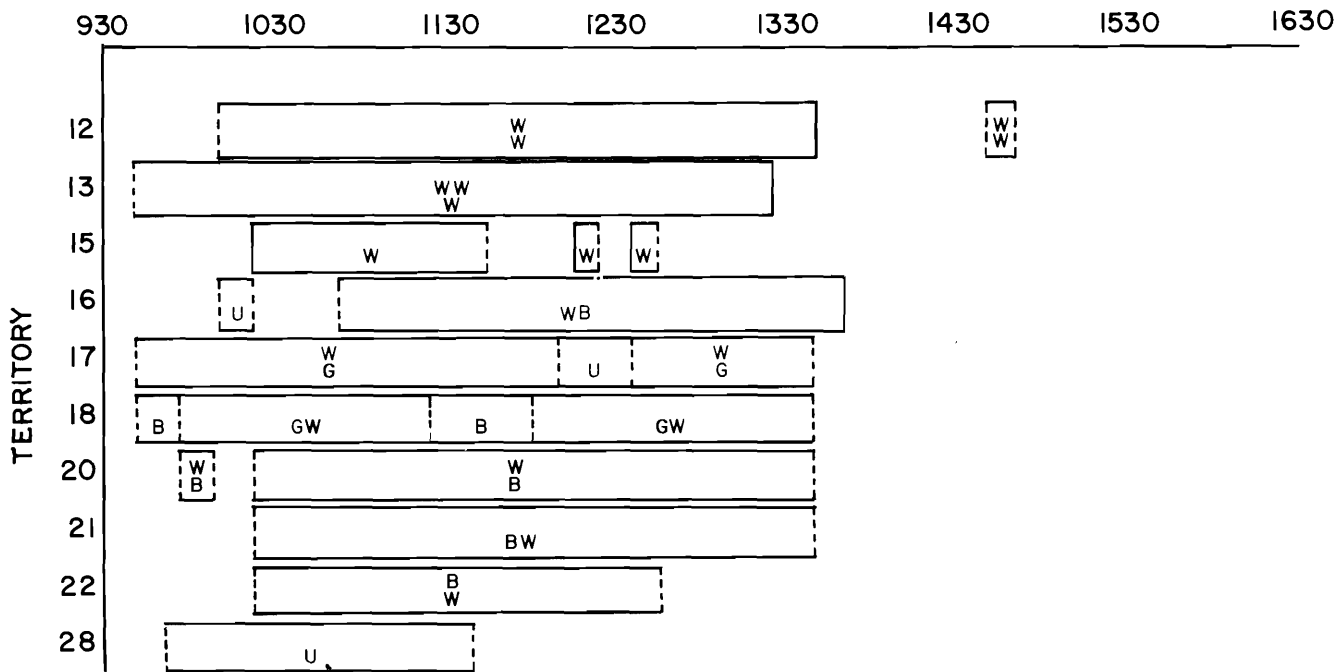
| | | AUGUST | | | | | | | | | | | | | | |
|-----------|----|--------|----|----------------|----|----|----|----|----|----|----|----|-----------------|----|-----------------|----|
| | | 5 | 6 | 7 ^a | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 ^a | 17 | 18 ^a | 19 |
| TERRITORY | 2 | O | RW | | RW | | RW | RW | RW | RW | RW | - | | - | - | - |
| | 3 | W | RY | | - | RR | RR | RR | RR | RR | RR | - | | RR | RR | RR |
| | 6 | R | R | | R | R | R | R | R | R | R | R | | R | R | R |
| | 7 | GR | GR | | U | U | - | - | - | - | U | U | | - | U | U |
| | 8 | BY | BY | | BY | BY | BY | BY | BY | BY | BY | BY | | BY | BY | BY |
| | 9 | OB | OB | | OB | OB | OB | OB | OB | OB | OB | OB | | U | U | U |
| | 10 | RW | RW | | RW | RW | - | - | - | - | - | - | | - | - | - |
| | 13 | - | - | | - | GY | BB | BB | BB | BB | BB | BB | | BB | BB | BB |
| 20 | - | - | | GR | GR | GR | GR | GR | GR | GR | GR | | GR | - | - | |

FIG. 6. Seasonal patterns of territory occupation by marked and unmarked (U) males of *Bombus rufocinctus* at the Montana site for 1 day in August 1987. Other letters refer to colour codes used for marked males. ^aRainy days on which no territories were occupied. ^bDays site not censused, but territories probably present.

A

Bombus rufocinctus

TIME



B

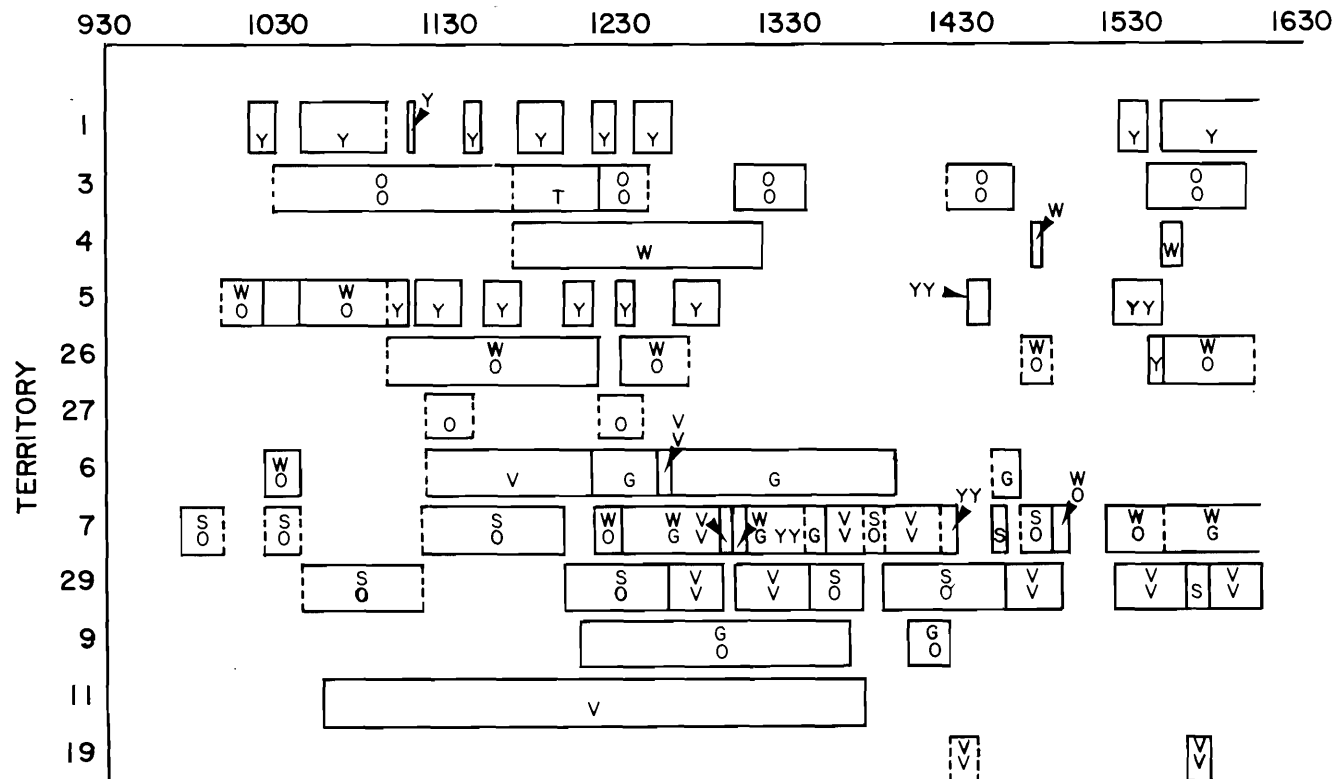
Bombus griseocollis

FIG. 7. Daily pattern of territory occupation by marked males of *Bombus griseocollis* and *Bombus rufocinctus* for 1 day in August 1987. Other letters refer to colour codes used for marked males. Broken vertical lines indicate estimated times.

1983), Montana, and Colorado populations of *B. nevadensis*, territories are often well separated from one another. In contrast, highly aggregated, sometimes contiguous, territories were the rule in the Virginia (Alcock and Alcock 1983) and Montana populations of *B. griseocollis* and in both populations of *B. rufocinctus* that we studied. However, we must exercise caution in our conclusions concerning *Bombus*, since some interpopulational differences in territory dispersion have been documented in the Hymenoptera (Evans and O'Neill 1988).

Males of three North American species, including two subspecies of *B. nevadensis*, are now known to exhibit territoriality. Our observations were similar to those obtained for *B. nevadensis auricomus* and *B. griseocollis* (Alcock and Alcock 1983). Males of two European species, *B. confusus* Schenck (Schremmer 1972) and *B. mendax* Gerstaecker (Haas 1976), and three species from Kashmir (P. H. Williams, personal communication) are also territorial.

Comparisons among territorial *Bombus* are of limited value at this point because of the small data base. However, some interesting comparisons with nonterritorial species can be made. Males of all territorial *Bombus* are characterized by enlarged, somewhat protuberant eyes and relatively large ocelli situated below the tops of the eyes. It seems likely that this form of compound eye is advantageous to males because it expands the visual field. Protuberant eyes occur in many ambush predators, such as mantids, and allow for a broad field of binocular vision (Frazier 1985). Linsley and Cazier (1972) note that enlarged compound eyes are common in male bees that search for females that pass above them, as do females of territorial *Bombus*. This form of compound eye is also characteristic of males of *Bombus* species whose behaviour has not been studied: the Palaearctic species *B. regeli* Morawitz, *B. vorticosus* Gerstaecker, and *B. niveatus* Kriechbaumer (Kruger 1951) and the North American species *B. crotchii* Cresson and *B. morrisoni* Cresson. However, enlarged eyes are not present in *Bombus* species in which other types of mating tactics have been documented.

Aside from the form of the eyes, the eight species of *Bombus* known to exhibit male territoriality are diverse morphologically. Seven of them are included in a cladistic analysis of *Bombus* based primarily on the male genitalia (Williams 1985). In Williams' phylogeny, they fall out on widely separated branches, suggesting that they be placed in two genera, *Mendacibombus* and *Bombus*, with the species of *Bombus* belonging in five separate subgenera. Each of the three species we studied is placed in a separate subgenus, *B. nevadensis* in *Bombias*, *B. griseocollis* in *Separatobombus*, and *B. rufocinctus* in *Cullumanobombus*. The subgenus *Cullumanobombus* also includes the European species *B. cullumanus* Kirby, which lacks enlarged eyes and is not territorial (Kullenberg *et al.* 1973). Among the species of bumblebees with males that patrol and scent mark flight circuits (Svennson 1980), there is a similar widespread placement in Williams' phylogeny. They fall within two genera, *Psythyrus* and *Bombus*, including eight subgenera of the latter. If this phylogeny is accurate, it suggests a high degree of convergence in male behaviour and morphology in bumblebees.

An association between scent marking and territoriality has also evolved independently in several other groups of aculeate Hymenoptera. In wasps, they occur in species of at least five genera of the sphecids subfamily Philanthinae (Evans and O'Neill 1988; O'Neill 1990) and in the vespids genus *Polistes* (Post and Jeanne 1980; Wenzel 1987). In anthophorid bees, the

release of a scent by territorial males has been reported in two genera. In some *Centris*, males scent mark plants in their territories with secretions from either the mandibular glands (Raw 1975; Vinson *et al.* 1982) or glands in the hindlegs (Williams *et al.* 1984; Coville *et al.* 1986). In several species of *Xylocopa*, territorial males release mandibular gland substances directly to the air after they have been transferred to the venter of the abdomen by the hindlegs (Velthuis and DeCamargo 1975a, 1975b; Marshall and Alcock 1981). In euglossine bees, territorial males apparently release chemicals previously collected from orchids and possibly modified by males (Kimsey 1980; Duffield *et al.* 1984). While scent marking is an obligate characteristic of territorial species of Philanthines, *Centris*, and *Bombus*, it appears to be absent in territorial males of nonphilanthine sphecids (Evans and O'Neill 1988) and in territorial hilltopping species of *Polistes* (Matthes-Sears and Alcock 1986) and *Xylocopa* (Alcock and Smith 1987).

The labial gland secretions of male *Bombus* that scent mark points along flight paths generally contain multiple components (up to 14), often encompassing a relatively wide range of molecular weights (reviewed in Duffield *et al.* 1984). Sympatric species differ in the types of chemicals used or in the proportions within multicomponent blends, as well as the location of flight paths and timing of male activity (Svensson 1980). Svensson (1980) suggests that the combination of these factors promotes premating isolation among sympatric circuit-flying *Bombus*. Preliminary analyses of the three *Bombus* we studied suggest that territorial species scent mark with chemical mixtures of very few components and that some sympatric species pairs use different chemicals. In other cases (i.e., *B. griseocollis* and *B. nevadensis* in Montana) territories occurred in different parts of the habitat.

As in the *Bombus* we studied, territorial males of many *Philanthus* (Evans and O'Neill 1988), of *Polistes fuscatus* (Fabricius) (Post and Jeanne 1983), and of *Centris adani* Cockerell (Frankie *et al.* 1980) show the highest rate of scent marking soon after arriving at territories each day. Alcock and Alcock (1983) also observed this in their studies of *Bombus griseocollis* and *Bombus nevadensis auricomus*. This pattern of scent marking may serve to provide a high concentration of chemicals early in the day that can then be maintained with a lower rate of scent marking. Given the great frequency of interactions among males in both *Philanthus* and *Bombus*, it seems likely that the chemicals deposited in territories attract females to territories and do not function as warning to conspecific males. In fact, other males may be attracted to the chemicals and subsequently attempt to usurp the territory (Evans and O'Neill 1988).

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