

CHEMICAL ECOLOGY OF BEES OF THE GENUS *CENTRIS*
(HYMENOPTERA: APIDAE)

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ABSTRACT

The reproductive biology of some plants is based on the movement of pollen between plants by insects. In many plant-insect pollination systems the plant produces a "reward" usually in the form of nectar. However, a number of plant taxa produce oil as a floral reward. Bees of the genus *Centris* are known as "oil-collecting" bees which are the important mediators in the reproductive success of oil reward producing flowers. These bees are solitary and their own reproductive success depends on the interaction between the sexes and the ability of the female to construct and provision a nest. In this paper we discuss the importance of male territoriality and its maintenance to the reproductive success of this taxa of bees. We also discuss the nesting biology of *Centris* in Costa Rica focusing on the resource needs of females.

Key Words: *Centris* reproductive biology, oil-collecting bees, male territorial behavior, bee nests.

RESUMEN

La biología reproductiva de algunas plantas está basada en el movimiento de polen entre plantas llevado a cabo por insectos. En muchos sistemas de polinización planta-insecto la planta produce un "agradecimiento" usualmente en forma de néctar. Sin embargo, cierto número de taxa de plantas producen aceite como agradecimiento floral. Las abejas del género *Centris* son conocidas como colectoras de aceite y son importantes mediadores en el éxito reproductivo de las flores productoras de aceite. Estas abejas son solitarias y su propio éxito reproductivo depende de la interacción entre los sexos y la habilidad de la hembra de construir y aprovisionar un nido. En este artículo discutimos la importancia del mantenimiento de la territorialidad del macho en el éxito reproductivo de estos taxa de abejas. También discutimos la biología de nidificación de *Centris* en Costa Rica haciendo hincapié en la necesidad de recursos de las hembras.

Pollen and nectar have long been recognized as important nesting resources for social and solitary bees (Baker & Baker 1975, Baker & Hurd 1968). As a result, female bees are essential to the reproductive biologies of many plants (Kevan & Baker 1983). However, some plants do not produce nectar, but produce lipids (Vogel 1969, 1974, 1976a, Seigler et al. 1978, Simpson et al. 1990). Solitary bees of the genus *Centris*,

which we have referred to as "Oil Baron Bees" (Vinson & Frankie 1991), are important pollinators of plants which produce lipid floral rewards rather than nectar (Buckmann 1987, Vinson et al. 1996, Vogel 1976b, 1981, 1986, 1988, 1990).

The floral oil reward pollination system was first described by Vogel (1974) and involves a number of plant species (Simpson 1989, Simpson & Neff 1981, Simpson et al. 1979), several of which are members of the family Malpighiaceae. Members of this family have glands on the abaxial side of the sepals called "elaiophores" (Fig. 1) that produce the oils (Anderson 1979). The oils are collected by a number of bees (Albuquerque & Rego 1989, Rego & Albuquerque 1989, Neff & Simpson 1991, Vinson et al., 1996), including species of the genus *Centris* (Hymenoptera: Apidae) which are considered important pollinators of these oil producing plant species (Simpson & Neff 1981, Simpson et al. 1977, 1990).

Although many species of Malpighiaceae are vines or shrubs (Gentry 1993), *Byrsonima crassifolia* (L.) D. C. is a moderate sized tree which produces a fruit known as Murici (Brazil) or Nance (Costa Rica) eaten by some people in Northern and Northeastern Brazil and in Central America (Braga 1976, Camargo & Mazucato 1984, Anderson 1983). *Byrsonima crassifolia* occurs from Paraguay to Mexico and may be composed of closely related segregates (Anderson 1978). The flowers of the Malpighiaceae are conservative among the species (Anderson 1979).

Of the 68 described species of *Centris*, 35 are known to occur in Costa Rica (Snelling 1974, 1984) of which 15 species have been collected in the Guanacaste Providence in dry forest region of Costa Rica (Snelling 1984, GWF & SBV unpublished data). Eight of these species are ground nesters and seven nest in pre-existing tree cavities made by other insects (Frankie et al. 1989; Table 1). Regardless of nesting site these

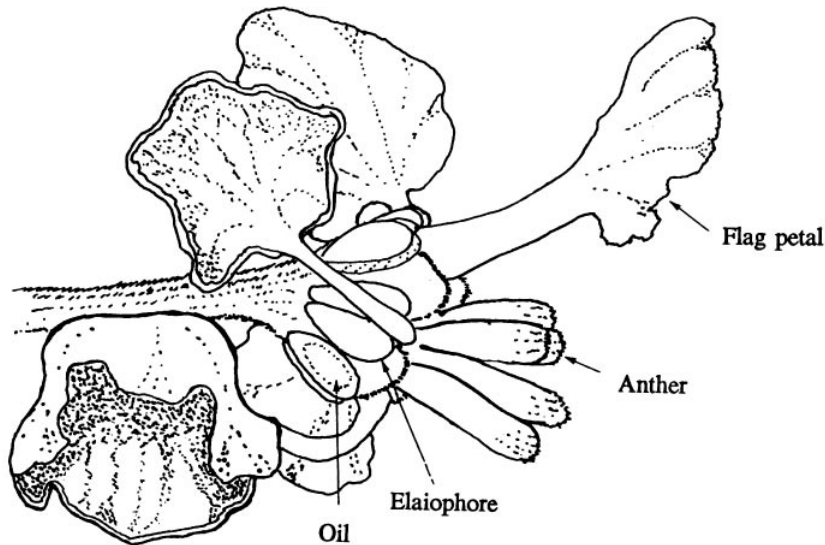


Figure 1. A diagram of a flower of *Byrsonima crassifolia* showing the location of the five pairs of elaiophores which produce an oil collected by several species of oil collecting bees. One petal, i.e., the flag petal, is grasped by the mandibles freeing the legs of the bee and allowing it to scrape the oil from the elaiophores.

TABLE 1. SUMMARY OF THE TERRITORIES OF MALE *CENTRIS* AND NESTS OF FEMALE *CENTRIS* IN THE DRY FOREST LIFE ZONE OF COSTA RICA.

Subgenera species	Territories				Nests				
	Mark ¹	Source ²	Height (m)	Area (m)	Plant Species ³	Nest ⁴ Substrate	Nest Depth (cm) or Hole Size (mm)	No. Cells	Comments
<i>(Centris)</i>									
<i>aethyctera</i>	0	—	3+	8-9	Ai, Cg, Cr, Co, Ca, Dr, Pr, Tb	Soil	8-14 cm	3-6	
<i>flavifrons</i>	3	MDG	2-5	6-12	By	Soil	50-108 cm	1	
<i>flavofasciata</i>	3	MDG	0.5	3-6	Ip	Sand		1	nest in sun
<i>aethiocesta</i>	3	MDG	1-3	3-6	Sm	Sand		1+	nest in shade
<i>inermis (= segregata)</i>	3	MDG	2-4	9-12	By	Bank	7-16 cm	1-6	
<i>adanae</i>	3	MDG	0.5	3-4	grass	Soil	3-10 cm	1	
<i>(Heterocentris)</i>									
<i>analis</i>	?	MDG	?	?	?	cav-wc	4.5, 6.5, 8 ⁵	3-6	=0.5 mm plug, thin oil
<i>bicornuta</i>	?	MDG	?	?	?	cav-wc	6.5, 8, 9, 5 ⁵	3-6	1-12 mm plug, thick oil

¹Level of marking indicated with 3 being frequent marking and 1 being infrequent; ²MDG = Mandibular gland; ³Plant species (N=nectar, P=pollen, O=oil); ⁴CAV = WC - cavity with wood chips; CAV - SA = cavity with sand; Bank - Embankment; rarely used; # = Number.

Co = *Cochlospermum vitifolium* (P)
 Cr = *Craetipina eriostachys* (N)
 Cu = *Caratella americana* (P)
 Dr = *Dalbergia retusa* (N)
 Gl = *Gliricidia sepium* (N)
 My = *Myrospermum frutescens* (N)
 Pr = *Pterocarpus rohrii* (N)
 Se = *Securidaca sylvestris* (N)
 Sm = Small bush
 St = *Stigmaphyllon ellipticum* (O)
 Tb = *Tabebuia* species (N)
 Tw = Twig

TABLE 1. (CONTINUED) SUMMARY OF THE TERRITORIES OF MALE *CENTRIS* AND NESTS OF FEMALE *CENTRIS* IN THE DRY FOREST LIFE ZONE

Subgenera species	Mark ¹	Source ²	Territories			Nests		
			Height (m)	Area (m)	Plant Species ³	Nest ⁴ Substrate	Nest Depth (cm) or Hole Size (mm)	No. Cells
<i>(Trachina)</i>								
<i>fuscata</i>	rare	?	2-5	4-9	Cb, Co	clay	?	
<i>heithausi</i>	1	TIBG	3-7	18-20	Cb, Se, Gl, Cg, My, Ce	soil	7 cm	2-6
<i>(Hemisiella)</i>								
<i>vittata</i>	1	TIBG	5-7	8-9	Cg	cav-sa	11	1-2 1-2 mm plug, thin oil
<i>nitida</i>	2	TIBG	2-15	8-9	By, Cg	cav-sa	8, 9.5, 11 ⁵	2-5
<i>trigonoidea</i>	2	TIBG	2-3	10-15	Tw	cav-sa	8	
<i>dichrotricha</i>	?	?	?	?	?	?	8	
<i>(Xanthemisia)</i>								
<i>lutea</i>	2	TIBG	0.5-2	20-30	grass	cav-wc	9, 9.5	3-5

¹Level of marking indicated with 3 being frequent marking and 1 being infrequent; ²MDG = Mandibular gland; TIBG = Tibial gland; Plant species (N=nectar, P=pollen, O=oil); ³CAV = WC - cavity with wood chips; CAV - SA = cavity with sand; Bank - Embankment; ⁴rarely used; # = Number.

Al = *Andira inermis* (N)
 By = *Byrsotoma crassifolia* (O)
 Ca = *Cordia alliodora* (P)
 Cb = *Cassia biflora* (P)
 Ce = *Cassia emarginata* (P)
 Cg = *Cassia grandis* (P)

Cr = *Caesalpinia eriostachys* (N)
 Cu = *Curatella americana* (P)
 Dr = *Dalbergia retusa* (N)
 Gl = *Gliricidia sepium* (N)
 My = *Myrospermum frutescens* (N)

Pr = *Pterocarpus rohrii* (N)
 Se = *Securidaca sylestris* (N)
 Sm = Small bush
 St = *Stigmaphyllon ellipticum* (O)
 Tb = *Tabebuia* species (N)
 Tw = Twig

bees require sources of nectar, oil, and pollen for their reproductive success and, therefore, are important pollinators of about 50% of all dry forest flowering plants that occur in the seasonal dry forest life zone (Frankie 1976, Frankie et al. 1976, 1990, Vinson et al. 1993). We have been interested in the chemical ecology of these bees focusing on two aspects, male territoriality and female nesting.

MALE TERRITORIALITY

Several reproductive strategies are employed by males to gain access to females (Alcock 1979, Emlen & Oring 1977). Among the acelate hymenoptera, these include female (nest) defense polygyny, resource defense polygyny, and landmark defense polygyny (Marshall & Alcock 1981, Eickwort & Ginsberg 1980). The latter, analogous to lek polygyny (Alcock & Smith 1987), generally involves a male aggressively defending a small area, driving off other males and releasing chemicals that both delineate the males space or "territory" and are, presumably, attractive to virgin females (Minckley et al. 1991, Frankie et al. 1980).

Territories of *Centris* vary considerably in their size, plant association, and male marking activity between species, although they have many features in common (Rau 1975, Frankie et al. 1989). Three species in Guanacaste, Costa Rica, *C. adanae* Cockerell, *C. trigonoides* Lepeletier, and *C. lutea* Friese defend territories in grass. *C. adanae* territories are usually less than half a meter above the ground in pockets of a shorter species of grass in which a small stick, shrub, or rock located near the center can serve as a perch (Frankie et al. 1980). The territorial area defended (Fig. 2) by *C. adanae* is about 3-4 m² although most of the activity occurs within a 1-2 m² space. Marking is frequent within the inner marking area and involves volatile compounds released by the mandibular glands (Table 2). In contrast, *C. lutea* establishes territories between 0.5 and 2 meters high at the tips of emergent jaragua grass, *Hyparrhenia rufa* (Mees.), an introduced species from Africa (Parsons 1976, Pohl 1983). These territories may encompass a defended 20-30 m² elliptical area with males perching on a grass seed head or shrub close to the upwind side of the defended area. Marking is less frequent and involves compounds released by glands located in the hind leg (Frankie et al. 1989; Table 3). Males of *C. lutea* have been observed on perches with their hind leg elevated so that the tibia and tarsi stick up (Fig. 3). This may provide a means of increasing the evaporation of compounds released by the tibial gland located in the hind leg in this species. Territories of *C. trigonoides* tend to be intermediate in the area patrolled (15 m²), and males tend to perch on twigs of leafless bushes that emerge above the jaragua grass (2-3 m), or they defend territories in *B. crassifolia* irrespective of whether the tree is in flower; these males moderately mark (Frankie et al. 1989). This species also has leg glands (Table 3) and spends more time hovering, often with its hind legs extended down (Fig. 4).

Territories of *C. flavifrons* Fabricius, *C. inermis* = *segregata* Friese, and *C. nitida* F. Smith (Table 1) tend to occur in downwind depressions in the canopy of *B. crassifolia* whether in flower or not, while *C. vittata* Lepeletier prefers the leguminous tree *Cassia grandis* Lb. *Centris flavofasciata* Friese males defend territories in coastal strand vegetation of *Ipomoea pes-caprae* (L.) R. Br. and *Canavalia maritima* (Aubl.), two species often referred to as Beach Morning Glory that are commonly intermixed and are similar in appearance (Wilson 1983). In all of these cases, the territories are initiated and defended during the morning. Males depart usually around noon. An exception is *C. aethiocesta* Snelling. A few *C. aethiocesta* male territories have been recorded in several species of small unidentified trees at the edge of the coastal strand. Male territorial behavior begins in the early morning soon after sun rises as is typical

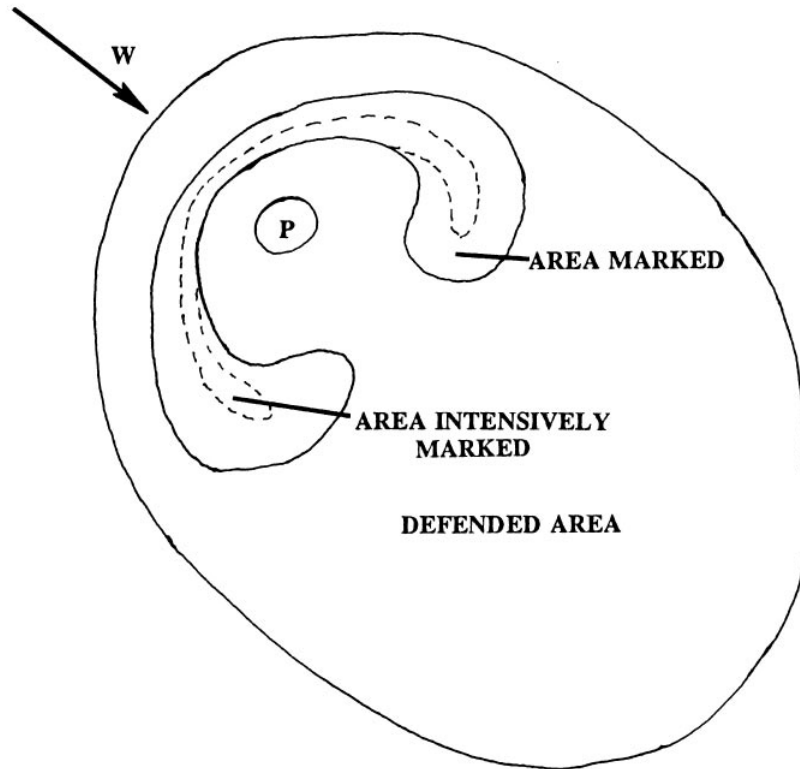


Figure 2. General territorial area of *Centris* displaying a form of lec defense polygyny reproductive strategy (based on male territories of *C. adanae*, *C. lutea*, and *C. flavifrons*). Distances depend on species and shape may be modified by local physical parameters. P = perch where the male may rest usually facing down wind. Area marked refers to the area where substrate marking may occur with the dashed area indicating where marking is more likely. Defended area is based on area where male will fly out to investigate an intruding bee-sized flying insect.

of the *Centris* species in Guanacaste. The *C. aethiocesta* territories were located on the ocean side of the bush as the breeze comes off the land. At about noon the males leave when the breeze usually stops. The breezes begin again about an hour later, but this time they come from the ocean side. Interestingly, the male bees return with the defended area of the territory on the land side of the bush. The territory is subsequently maintained for about three hours (SBV, unpublished data).

Although most of the male *Centris* prefer to defend territories in only one or two species of plants (Table 1), several species of *Centris* utilize a wide variety of plants. For example, *C. heithausi* Snelling can be found in downwind depressions in the canopy of *C. grandis*, *Myrospermum frutescens* Jacq. (Frankie et al. 1989), *Gliricidia sepium* (Jacq.) Steud., *Piscidia carthagenensis* Jacq., *Cassia emarginata* L., *Securidaca sylvestris* Schlecht, and *Cochlospermum vitifolium* (Willd) Spreng (Coville et al. 1986). However, most territories occur in *G. sepium* when it is in flower and then shift

TABLE 2. CHEMICAL COMPOSITION OF THE MANDIBULAR GLANDS OF TERRITORIAL MALE *CENTRIS* FROM GUANACASTE, COSTA RICA (VINSON ET AL. 1982, 1984, 1989).

Species	Chemical	% Total
<i>C. adanae</i>	Geraniol	80.0
	Geranyl acetate	17.2
	Nerol	0.8
	Ethyl laurate	0.6
<i>C. flavifrons</i>	Geraniol	77.0
	Geranial	10.1
	Neral	7.2
	Geranyl acetate	2.3
	Nerol	T ¹
<i>C. flavofasciata</i>	Neral	56.7
	Geraniol	17.2
	Geranyl acetate	16.4
	Geranial	9.7
<i>C. aethiocesta</i>	Neral	57.8
	Geraniol	15.8
	Nerol	13.4
	Linalool	9.8
<i>C. inermis</i>	Geraniol	73.7
	Geranial	15.3
	Neral	6.7
	Nerol	1.7
<i>C. inermis</i> (<i>segregata</i> morph)	Geraniol	45.2
	Geranial	42.9
	Neral	9.2
	Nerol	2.6

¹T = Trace.

to the other plants which come into flower as flowering of *G. sepium* declines. Marking is not common in *C. heithausi* Snelling (Table 1).

Centris aethyctera Snelling also defends territories in a number of different tree species (Table 1), usually during flowering. No marking by *C. aethyctera* has been observed (Frankie et al. 1989). The observations suggest that both *C. aethyctera* and *C. heithausi* have evolved to patrol territories where they can intercept females seeking nectar. *Centris fuscata* Lepelletier may also employ a similar strategy since it rarely marks, but *C. fuscata* tends to defend in either of two important pollen resources during their blooming period (Frankie et al. 1989). As shown in Table 1, the males of each

TABLE 3. CHEMICAL COMPOSITION OF THE TIBIAL GLAND LOCATED IN THE HIND LEG OF TERRITORIAL MALE *CENTRIS* FROM GUANACASTE, COSTA RICA (WILLIAMS ET AL. 1984).

Species	Chemical	% Total
<i>C. heithausi</i>	Pentacosene	37.0
	Nonadecadiene	21.0
	Heptadecene	15.0
	Tetradecenyl acetate	9.0
	Pentacosane	5.0
	Heptadecane	3.0
	Heptacosane	3.0
	Other hydrocarbons (4)	6.0
<i>C. nitida</i>	2-Pentadecanone	53.0
	2-Heptanone	32.0
	Tetradecyl acetate	9.6
	Ethyl myristate	3.7
	Ethyl palmitate	1.7
	Hexadecyl acetate	T ¹
<i>C. trigonoides subtarsata</i>	2-Pentadecanone	53.0
	Hexadecyl acetate	34.9
	Ethyl myristate	8.6
	Ethyl palmitate	3.5

¹T = Trace.

species can be recognized based on their plant association, size of territory, and their territorial behavior. In spite of similar preferences for certain plants, such as *B. crassifolia* or grass, territories rarely overlap (Frankie et al. 1989).

The territorial pheromones of the species employing a landmark defense strategy are produced in either mandibular glands or glands located in the hind legs (Frankie et al. 1989). As can be seen in Table 2 and 3, each species has its own pheromone blend but those having mandibular glands have terpenes, alcohols, aldehydes, and esters while those with leg glands tend to be composed of hydrocarbons, ketones, and fatty acid esters. Males of *C. analis* Fabricius and *C. bicornuta* Mocsáry are not included in Table 2 because they are difficult to distinguish and variation in our samples has suggested a mixture of species, thus this data is not provided. Data for *C. lutea* is based on only one specimen and is not included. Male territories of *C. dichrotricha* (Moure) have not been found.

The territorial chemicals from *C. inermis* and *C. segregata* (Vinson et al. 1984) are of particular interest because both male and female *C. segregata* are distinct color morphs of *C. inermis* and were considered a separate species until Snelling (1984) recognized *C. segregata* as a synonym of *C. inermis*. We observed that territories of *C. inermis* in *Byrsonima* in the early dry season were often replaced by the *segregata* morph of *C. inermis* later in the dry season. We also reported the chemistry differed

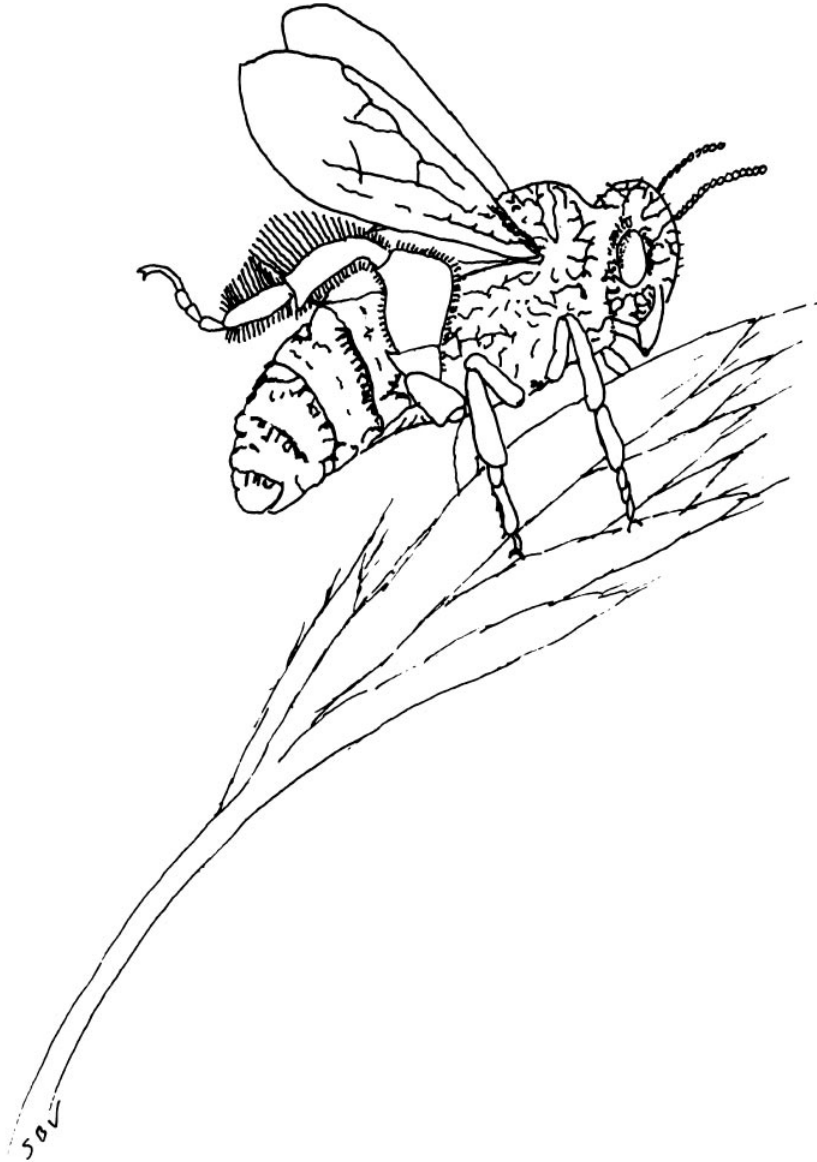


Figure 3. Diagrammatic representation of *Centris lutea* perched on a grass head with his hind leg extended up into the air stream. The hind leg is the source of a territorial marking material.



Figure 4. Territory of a male *Centris trigonoides* in *Byrsonima* showing the extension of the hind leg (arrow) where a pheromone is released while hovering.

in the two morphs, but primarily in the percent composition of the two major compounds (Vinson et al. 1984), rather than different compounds (Table 2).

In many *Centris* species, such as *C. inermis*, *C. flavifrons*, and *C. flavofasciata* in Costa Rica and *C. pallida* W. Fox in the southwest United States, metandric forms (sometimes referred to as "beta" males) occur. These males are larger than the territorial males and appear to patrol nest sites where they have been reported to wait for females and to mate as they emerge or to even attempt to dig them up to mate (Alcock et al. 1976a, 1977, Chemsak 1985, Toro et al. 1991). In *C. pallida* beta males have been observed to be successful while the smaller alpha males defending territories in bushes nearby rarely appear to intercept females (Alcock et al. 1977, Rozen & Buchmann 1990).

Both the beta male strategy of searching for and digging up emerging females and the alpha strategy of releasing pheromones and defending territories, appear to be energy intensive (Vinson et al. 1982). As shown by Frankie et al. (1980), the nectar content in the crop of male *C. adanae* significantly decreased during the time males spent in the territory and the crop was nearly empty when these males abandoned their territorial activity around noon. Males of all the *Centris* species in the area can be collected from a number of nectar sources in the early afternoon, including the plant species indicated in Table 4. Thus, male *Centris* are also important pollinators of these massively blooming nectar reward trees.

TABLE 4. THE RESOURCE NEEDS OF *CENTRIS* FROM THE DRY FOREST OF COSTA RICA.

<i>Centris</i> Needs	Source	Function
Nectar ¹	Ai, Dr, Pr, My, Se, Tb, Cl, Cr	For maintenance. For nest provisions (some species).
Pollen ¹	Ca, Cb, Ce, Cg, Co, Cu	For nest provisions.
Oil I ¹	By	For nest provisions (some species). For sand collection. For wood chip collection.
Water (some situations)	Ponds and streams	For sand collection. For wood chip collection.
Sand	River banks, wind rows	For cell wall construction (some species).
Wood chips	Wood boring insects	For cell wall construction (some species).
Resin I	?	For cell wall construction.
Oil II	?	For nest defense (some species).
Resin II	?	For nest defense (some species).

¹See Table 1 for plant names.

NESTING BEHAVIORS

In studies of the chemical ecology of nesting, there are several questions to be explored. First, nests must be located and the nesting substrate and morphology of nests described. Secondly, the source of the materials used to construct the nest and cell(s) must be determined. Thirdly, the resources collected or produced to provision the cells, to mark the nest and for use in nest defense must be determined. However, these questions are particularly challenging due to the known diverse nesting habits and reproductive strategies of the genus (Michener & Lange 1958, Coville et al. 1983).

The diversity in nesting habits ranges from the production of solitary nests where only one cell is provisioned as occurs in *C. adanae* (Frankie et al. 1989), through solitary nesting with provisioning of several cells as occurs in *C. fuscata* (Raw 1984), to aggregated nesting with several cells per nest as occurs in *C. pallida* (Alcock et al. 1976b, Rozen & Buchmann 1990). Nests may occur in flat ground or earthen banks (Vinson & Frankie 1977, Batra & Schuster 1977) or females may utilize existing holes in wood, but with specific preferences for certain habitats (Frankie et al. 1988). Other species nest in termite nests (Bennett 1964, Pickel 1928) or in the tumulus of *Atta* ant nests (Vesey-Fitzgerald 1939). *Centris flavifrons* prefers to initiate a nest in a depression in the soil and is frequently found to have nest entrances in the side of burrows excavated by *Ctenosaura similis* (Vinson & Frankie 1988), a common iguana lizard that also nests in the soil during the dry season (Fitch & Harkforth-Jones 1983). Thus, the location of the nests of a particular species, for the first time, is often a product of

chance and patience. Further, *Centris* show some adaptability. For example, *C. aethyctera* usually excavates a single linear tunnel in which 3-6 cells, one on top of the next, are provisioned (Vinson & Frankie 1977), but in rocky soil or under poor resource conditions the nest may consist of several cells together in a pocket in the soil or only one or two cells (Vinson & Frankie 1991).

When we began these studies, there was no data on the nesting of any of the species in Costa Rica. Within a few years we had discovered nests of six of the eight species which we now know nest in the soil, but had not yet determined the rearing habits of *C. inermis* and *C. segregata*. In 1981 we discovered a mixed nesting aggregation of *C. segregata* and *C. inermis* in a river bank. The nests of each species were marked, the nests described, and some of the cells from each were collected and transported to the laboratory. All the collected cells yielded *C. segregata* even though some had been clearly provisioned by *C. inermis* (Coville et al. 1983). These results led Snelling (1984) to reevaluate the characters of these two species and to synonymize *C. segregata* with *C. inermis*.

There were indications that some *Centris* would nest in cavities in wood (Jayasingh & Freeman 1980, Kimsey 1978), and even though we had looked in dead trees, we still lacked nests for seven species. In 1980 we discovered a *C. vittata* nesting in a cavity in a tree stump. Although *C. vittata* had been observed to nest in existing holes in earthen banks, and species of *Hemisiella* and *Heterocentris* appeared to adopt a variety of cavities as nest sites (Coville et al. 1983), this was our first evidence that some of the Costa Rican species did nest in wooden cavities. This led to an effort to produce artificial nesting sites in which holes drilled into wood would be tested to determine if some species could be induced to nest. The technique was successful and tests in 1981 using nest blocks with holes of different sizes produced nests of the remaining seven species (Table 1).

All the members of the subgenera *Centris* and *Trachina* in Costa Rica nest in soil, but each species has different requirements (Frankie et al. 1989, Table 1). However, all initially form tunnels of a particular length depending on the soil and species. For example, *C. aethiocesta* excavates a 6 cm tunnel in sand while *C. flavifrons* tunnels may be 108 cm long in sandy clay loam (Vinson & Frankie 1988). Further, depending on species, one or more cells may be formed with the first placed at the end of the tunnel and with the rest placed sequentially on top. The cells consist of a waxy-resinous-like material embedding several millimeters of the surrounding soil. These cells are provisioned with pollen filling about one-third to one-half of the cell. A liquid is then added covering the pollen to a depth of 3-4 millimeters. Then an egg is oviposited which floats on the liquid. The cell is capped with what appears to be the same resin-waxy material mixed with the surrounding soil. When the appropriate number of cells have been provisioned, the female fills the remaining tunnel with loose soil (Vinson & Frankie 1977, 1988, 1991, Vinson et al. 1987).

The remaining subgenera nest in cavities in wood which are probably produced by wood boring insects. Each species prefers a certain size entrance hole (Frankie et al. 1988, Table 1) and habitat (Frankie et al. 1988, 1993). The cavity nesting species can be separated further on the basis of the material used to build the cells and to fill spaces between cells. The three species of the subgenus *Hemisiella* use sand while both the subgenera *Heterocentris* and *Xanthemisia* use wood chips. Several of these wood cavity nesting species leave an oily or resinous deposit near the nest entrance (Fig. 6) after the last cells has been completed (Frankie et al. 1988, 1989, Table 1).

From the above discussion it is clear that female bees must collect a number of resources. These include nectar for their own energy; a liquid to mix with the soil to construct the cells, or in the case of some wood cavity nesters, to mix with wood chips or sand; pollen to provision cells; a liquid to add to the pollen provisions; and resins and

oils to seal the entrance of nests. However, the source and nature of some of these materials is not clear (Table 4).

Pollen

Pollen is an essential provision providing the protein required by the developing bee. Several plants that bloom during the dry season are known to be important excess pollen producers (Table 4). These include *Cochlospermum vitifolium*, *C. grandis*, *C. biflora* L., *C. emarginata*, *Curatella americana* L., and *B. crassifolia* (Frankie et al. 1983, 1989), although which species are used most frequently by the different bee species as a pollen resource has not been determined.

Oil

Centris have been referred to as oil collecting bees and all the 16 species found in the dry forest life zone of Guanacaste have been observed collecting oil from *Byrsonima* (Vinson et al., 1996). Vogel (1974) first postulated that floral oils could be used instead of nectar for larval development, but gave no evidence. Simpson et al. (1977)

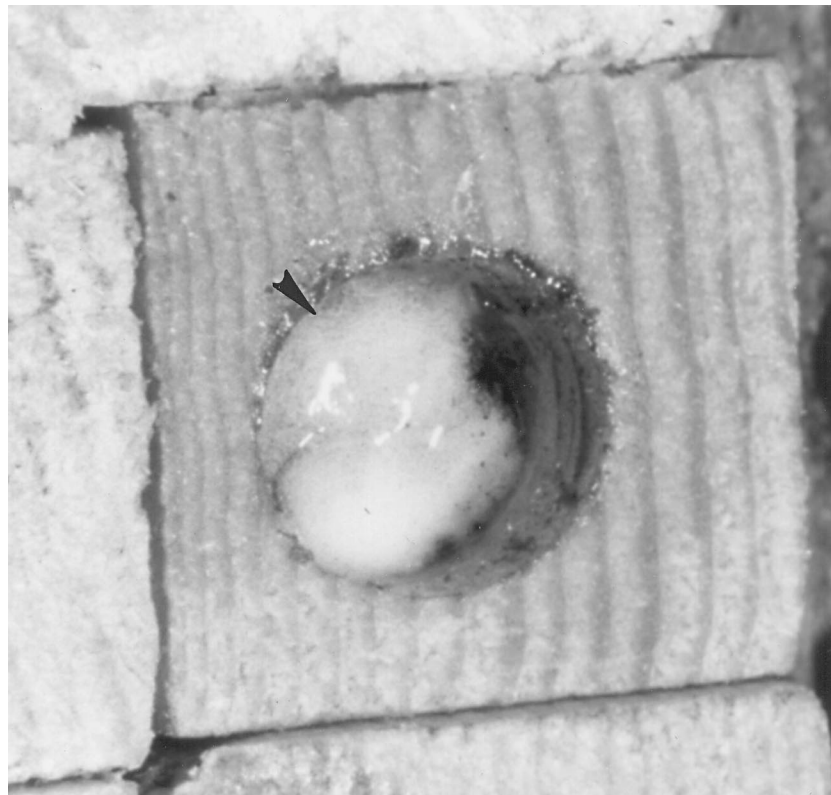


Figure 5. A wooden bee trap nest block showing the entrance to the completed nest of *Centris bicornuta* plugged with a "mayonnaise-like" oil (arrow).

reported that the nest cell provisions of *C. trigonoides*, a cavity nester, consisted of pollen and floral oil with no appreciable carbohydrate. Neff & Simpson (1981) reported that another species, *C. malcutifrons*, in Peru provisioned their cells with pollen and oil, along with "appreciable" amounts of nectar. This led Neff & Simpson (1981) and Simpson et al. (1990) to question the absence of nectar in the nest provisions of *Centris*.

To determine whether the *Centris* in Costa Rica use only oil, we first examined the oil produced by *B. crassifolia*, and we found two different oil types. Most of the trees we sampled were found to produce a mixture of mono-, di- and tri-glycerides and free fatty acids (Vinson et al., 1996). The mono-glycerides composed over 50% of the oil with the di-glycerides being the second most abundant compounds. The tri-glycerides made up only 10% while the remaining 5% consisted of a mixture of free fatty acids. The fatty acids released from the glycerides by de-esterification consisted of saturated C16-20 and unsaturated C18-22. A nearly identical glycerol ester and fatty acid composition was found for the liquid in cells of *C. aethectera*, *C. flavifrons*, *C. flavofasciata*, and *C. adanae*, the only four ground nesting species examined (Vinson et al., 1996, Table 5).

The oil from some *B. crassifolia* trees contained an abundant unknown that was considerably more polar than the glycerides reported above and yielded two unidentified GC peaks on de-esterification. No bee cells containing this lipid pattern were found, but the sample size was limited (Vinson et al. 1996). Whether only certain trees produce this oil with the unknowns, or the same tree produces both types but at different times or under different conditions, is now under study.

We recently collected the liquid contents of five cells of *C. bicornuta*, a wood cavity nester, just after completion and before the embryo hatched. Unlike the oil from *B. crassifolia* or the liquid content of the cells of the ground nesters, the liquid from the *C. bicornuta* nest cells was not soluble in hexane and no lipids were detected. However, the liquid consisted of carbohydrates (SBV, GWF, & HJW, unpublished data). Thus, *C. bicornuta* uses nectar along with pollen to provision their cells (Table 5).

Since *C. bicornuta* has been observed collecting oil, its use is a major question. In the process of opening many *C. bicornuta* nests, it has been observed that wood chips fill spaces between cells, and in bigger diameter cavities the space between the cells and the cell wall also consisted of wood chips. These chips were sticky and the sticky material was soluble in hexane. An analysis by TLC (Vinson et al. 1996) revealed a lipid pattern, when exposed to I₂ vapor, similar to *C. crassifolia* oil, but with several additional spots, depending on the sample. These additional trace compounds, which

TABLE 5. COMPOSITION OF NEST CELL CONTENTS OF SIX *CENTRIS* SPECIES.

Species	Provision Composition	
Ground nesters:		
<i>C. adane</i>	Pollen	Oil
<i>C. flavifrons</i>	Pollen	Oil
<i>C. flavofasciata</i>	Pollen	Oil
<i>C. aethectera</i>	Pollen	Oil
Cavity nesters:		
<i>C. bicornuta</i>	Pollen	Nectar

remain unidentified, varied and may come from the different woods that are the source of the wood chips. The collection and transport of sand to their nests by *C. nidita*, *C. trigonoides* (Fig. 7), and *C. vittata* on their legs was reported by Vinson et al. (1993). The transported sand around and between the cells of *C. nidita* was also found to be sticky in most nests, and the sand from these nests rinsed in hexane yielded a TLC pattern nearly identical to *B. crassifolia* oil. We suggest that females use the oil to stick the wood chips or sand to their legs to aid in the transport of these materials to the wood cavity.

In a few nests, neither the wood chips or sand were sticky and no oil could be detected. We (SBV & GWF, unpublished data) have observed *C. nidita* and either *C. analis* or *C. bicornuta* (impossible to tell apart unless captured and examined) landing at



Figure 6. Picture of *Centris trigonoides* in a sand pit collecting sand for nest construction.

the edge of a stream and dipping their hind legs into the water and flying off. This may be an alternative to the use of oil to transport sand or wood chips and may be more common when oil is unavailable (Table 4).

The entrance to completed nests of *C. bicornuta* and *C. vittata* are covered with an oily material that appears similar in consistency and color to whipped oil or "mayonnaise" (Fig. 6). A similar material has been observed on rare occasions at the entrance of completed nests of *C. nitida*. In *C. vittata* after one, two, or three cells are provisioned, a partial cell is constructed and the inner surface is coated with a similar oily material. In *C. bicornuta* after a series of 2-6 cells are completed, the female constructs a plug of material of similar consistency as a cell. This plug is generally over 6 mm thick. There is usually some space between the last completed cell and the plug. The plug is usually recessed 4-6 mm and this space is filled with an oily material (Fig. 6). Observations of 16 *C. bicornuta* females developing this oily plug suggests the female brings in a liquid on her scopae which she removes at the entrance. She then turns around and appears to add a regurgitate. She then again turns around and sticks the tip of her abdomen into the material and rapidly twists her abdomen in a whipping motion appearing to add air to the mixture and to whip the material into a "mayonnaise" like material. Although a number of bee components are likely added, the TLC pattern has no resemblance to *B. crassifolia* oil. The source of the initial liquid (Oil II) is unknown (Table 6). This material hardens over a period of several days to resemble a crumbly cheese which persists for a year.

The cell wall of most *Centris* nests is composed of either soil, sand, or wood chips embedded in a hard waxy-resinous-like material of unknown origin. The suggestion has been made (Vogel 1974, Neff & Simpson 1981, Simpson 1989, Buchmann 1987) that the cell is composed of oils collected from such plants as *B. crassifolia* to which secretions are added to cause the hardening and the material is mixed with the soil or wood chips and hardens. However, we have been unable to support this suggestion, although the source and nature of the material remains unknown. Our evidence is based on observations of the nesting behavior of *C. flavofaciata* (SBV & GWF, unpublished data) which only begins to construct a cell when returning with a brownish liquid on her scopae.

Females of *C. flavofaciata* construct a tunnel and then construct a single cell at the end of the tunnel. This cell is provisioned, capped, and then the tunnel is then filled with sand (Vinson et al. 1987); the process requires about one day. Females initiating a nest in the evening complete the tunnel, prepare the cell chamber, and then wait until dawn to begin to construct a cell. By digging up nests before and after the first morning trips were made by the bee (SBV & GWF, unpublished data), we determined that no cells were initiated before the first trip; however, nests dug up during the bees' second trip had the base of the cell formed. The partially formed cell was soft with the sand being oily and the binding material soluble in ethanol, but not hexane. After the bee made 3-4 trips, the cells were almost completely formed although they remained soft. Bees collected during these trips to the nest had their scopula filled with an oily material that hardened with time (4-6 h) and was soluble before hardening in ethanol, but not hexane.

We tried to determine if females added something by examining the crop, Dufour's gland, labial glands; we also examined females for other possible glands. Dissections of bees returning upon the first trip had a full crop that appeared to contain nectar (it did not harden) that was partly soluble in ethanol (becoming cloudy). The Dufour's gland of *C. flavofasciata* is similar to that of *C. flavifrons* which is reported by Cane & Brooks (1983) to be a long, thin tubular gland. The Dufour's gland showed no differences in size between the first and fifth trip. Further, Cane & Brooks (1983) reported that the Dufour's glands of several *Centris* contain a series of hydrocarbons. Hydro-

carbons are not very reactive and are soluble in hexane. The small mandibular and labial glands also appeared identical in bees collected on the first and fifth trip back to the nest. No other obvious glands were found. The fecal material in the hind gut was not completely soluble in water, ethanol or hexane and when mixed with the oil of *B. crassifolia* did not result in hardening. These observations, along with the natural hardening of the material on the females scapula, suggest the females collect something (Resin I) that hardens without female additives (Table 4). Further, the suggestion that *B. crassifolia* oil is the base material used in cell wall production (Simpson 1989, Neff & Simpson 1981, Buchmann 1987) is not supported unless the *B. crassifolia* oil from some trees is substantially different. Although substantial differences in *B. crassifolia* oil from some *B. crassifolia* trees was reported (Vinson et al., 1996), the oil containing the large amount of an unknown also is soluble in hexane and does not harden over time, suggesting this oil is also not responsible. Thus, the source of the cell soil or wood chip binding material remains unknown.

Resins

Whether the cell wall material is an oil or resin awaits further analysis. Resins are used by a species of *Anthodioc* and a species of *Chalicodoma* that also nest in our wooden nest blocks.

The source of the various resins and oils is difficult to determine. The TLC separations of the ethanol soluble cell wall material of *C. flavofaciata* indicates a complex mixture; and while the cell wall material appears physically similar among the ground nesters, the cell walls of tree nesters have some slight differences which may or may not be due to the presence of a small amount of *B. crassifolia* oil. More important than the chemical composition, is the sources of these materials. The population of these oil-collecting bees appears to be in decline (Vinson et al. 1993). The reason for the decline is not clear, but a reduction in any one of the resources required by these bees could be responsible. However, there are several pollen and nectar sources (Table 4), and these are probably not resource limits. The situation with the Oil I used in nest provisioning is less clear. There are several species of Malpighaceae in the area (Vinson et al. 1993) that may provide usable oil for some of the tree cavity nesting species as indicated in Table 5, and the oil may not be the limiting factor. However, the resin used for constructing the cell could be limiting if all the *Centris* species in the dry forest depended on a particular plant. The problem is to determine the source of the cell wall material. There are many resins and gums released by a variety of trees attacked by various insects along with many other resin and gum compounds associated with plants. Although a number of these materials have been collected from nests and the chemical composition of some of these are partially known, knowing the chemistry may not be very helpful since the chemistry of only a very small percent of the possible resins, gums, and other plant exudates are known. Thus, knowing the chemistry of the cell material or defensive materials may be of little help in identifying the important resources, particularly if combinations are used. It is only through a complete knowledge of the resource needs of these bees that efforts can be made to insure their survival in the remaining Pacific dry forest which is also under threat from a variety of forces (Vinson & Frankie 1993).

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