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THE ECOLOGICAL SIGNIFICANCE OF AN ARBOREAL NEST OF *BOMBUS PULLATUS* IN COSTA RICA¹

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ABSTRACT

A *Bombus pullatus* nest 5.5 m above the ground in the foliage of a banana plant was collected at 1,400 m elevation near San Vito de Java, Costa Rica. Containing 36 presumably virgin queens, 259 workers, and 48 males, the colony has certain traits suggesting perenniality or mobility. It is postulated that the failure of bumble-bees to attain an abundance in the wet lowland tropics equivalent to that in temperate mesic habitats may be due to a shortage in tropical habitats of dry underground cavities plus the ephemeral nature of arboreal nest sites, increased predation on both individual bees and entire nests, and increased competition for arboreal nest sites by smaller social bees and ants.

This brief discussion of a tropical bumble-bee and its nest is offered in hopes of generating interest in the ecological question of why bumble-bees are rare in wet tropical lowlands. In Costa Rica, *Bombus pullatus* Franklin is locally common to rare, but the high density sites occur only between 1,000 and 1,800 m elevation in areas with 2 to 3 m of rainfall and a mild dry season (e.g., the area around San Vito de Java and Monte Verde, Puntarenas Prov., the slopes above San Isidro del General, San José Prov., the passes between Naranjo and Villa Quesada, Alajuela Prov.). In such areas of high bee density, workers and queens occur at all times of the year. The relative abundance of queens varies strongly with the season, but workers may be regularly encountered at their usual host plants (*Solanum*, *Stachytarpheta*, *Cassia*, various Lobeliaceae and Melastomataceae, etc.) with at most an hour's search. Above 1,000 m elevation, *B. pullatus* is sometimes sympatric with two other Costa Rican bumble-bees, *B. ephippiatus* Say (very common) and

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B. volucelloides (rare). However, in the wet lowlands of Costa Rica (primary and disturbed rainforest), *B. pullatus* occurs consistently but very rarely throughout the year (e.g., the area around Rincón, Osa Peninsula, Puntarenas Prov., the area around Florencia and Puerto Viejo, Sarapiquí Dist., Heredia Prov.). At these lowland sites it is the only bumble-bee present; *Euplusia*, *Eulaema*, *Xylocopa*, and several genera of Anthophoridae are the only other large bees in the same habitat. *B. pullatus* ranges from Costa Rica southward into Venezuela, the Guianas, Colombia, Peru, Ecuador, Bolivia, and Brazil (Milliron, in lit.).

The nest of *B. pullatus* has not been described. Only a few other tropical bumble-bee nests and nesting behaviors have been described [e.g., *B. incarum* Franklin, Brazil, Dias, 1958; British Guiana, Myers, 1935; *B. morio* (Swederus), Brazil, Milliron, 1961; *B. atratus* Franklin, Brazil, Sakagami et al., 1967; Dias, 1960; *B. medius* Franklin, Mexico, Michener and LaBerge, 1954; Rau, 1941; *B. opifex* Smith, Peru, Janvier, 1955; see also references in Moure and Sakagami, 1962]. Only one nest (Dias, 1960) was arboreal (1.2 m above ground in a bundle of dry grass). The other nests were on the ground surface or in very shallow holes. However, Gaumer (in Bequaert, 1932a) says that *B. medius* may nest in hollow trees on the Yucatán peninsula. Frison (1930a, b), Pitelka (1954), Sladen (1912), Bequaert (1932b), Howard (1918), and Gibson (1930) report occasional *Bombus* nests in arboreal bird nests in temperate areas. However, it is clear from the *Bombus* literature that most temperate zone bumble-bee nests are subterranean, or if above the ground, in very substantial structures like stone walls and buildings.

I collected a nest of *Bombus pullatus* on June 22, 1969, about two months into the rainy season. It was 5.5 m above the ground in the top of a banana plant (*Musa*) in a half-acre banana planting on Finca Las Cruces, about 8 km south of San Vito de Java, Puntarenas Prov. (1,400 m). The site was 100 to 300 m from large expanses of old secondary succession bordered by cattle pastures and coffee plantations. One large banana plant tipped into the crown of another formed an open tangle of live and dead leaf blades and upper petiole ends. One of the dead leaves was bent at the base of the blade, and the mass of *Bombus* cells was perched on the upper side of the bend in the petiole which was approximately 10 cm wide. The roof and two sides of the nest cavity were formed by other banana leaves and petioles whose edges were sealed together with a thin mache made of fibers from banana leaves, mud, and resins or waxes of undetermined origin. The third wall (15 cm tall, 20 cm wide, 1–4 mm thick) was made purely of this mache, and the cells were fully visible through the entrance (10 cm tall, 15 cm wide). The entire cavity had a volume of 1 to 2 liters. The nest was in broken shadow during the day and sheltered from direct rain by banana leaves.

The first bees left the nest approximately 45 minutes before sunrise and the last returned about the same interval after sunset. At these times, they were barely visible against the sky. A light tapping on the

banana trunk in daylight hours caused 5 to 15 bees immediately to leave the nest and buzz around the general area within 3 to 10 m from the nest; a person moving in this area was usually stung.

The nest was too well ventilated for successful use of ether, and so the colony was collected at night by cutting the banana trunk and picking up the bees from the ground where the nest had fallen. Many workers and some queens were very aggressive: they flew or crawled upward on pantlegs and stung the collectors. Some (especially queens) tried to escape by crawling down into the grass and not buzzing when pressure was applied to their hiding places. No more bees were found at the site the next day. Almost all of the bees in the colony were collected (36 queens, 259 workers, and 48 males). All queens collected had entire wing margins (many workers had worn wing margins), suggesting that the queen was missed or had died. During the following week, 9 queens and 11 males emerged from the cells. The 363 bees collected directly from the nest were preserved in alcohol and have been deposited in the Snow Entomological Museum, University of Kansas.

This colony was in the sexual reproduction stage of its development. In 142 unhatched cocoons, there were 26 queens, 109 males as live adults or fully pigmented pupae, and 7 dead male pupae. The 18 small larvae (about $\frac{1}{4}$ the weight of full-grown larvae) were single in wax cells. Queen cocoons were about 22 mm long and 16 mm in diameter, and male cocoons 16 by 12 mm. Of the 135 unhatched cocoons of reproductives, only three were intermediate in size between the sexes, and these contained large males. There were no intermediates among the 172 hatched cocoons (65 queen cocoons, 107 male cocoons). The workers of *B. pullatus* are distinctly smaller than the males, and worker cocoons would, therefore, probably be noticeable as a third size-class. Assuming no cocoons had been destroyed, this colony would have produced 91 queens and 216 males in this reproductive season, of which 32 and 27% (respectively) had already left the nest. Emergence of queens and males was relatively synchronous within clusters of 5 to 15 cocoons. In some clusters all or part of the males had emerged, in others, all or part of the queens. Clusters ranged in content from 11 males to 1 queen, to 6 males to 5 queens, to 3 males to 10 queens. Ten open or wax-capped cells, each containing 1 to 2 cc of "honey" were found in the nest. Four queen-sized cells were packed full of pollen from at least eight species of plants.

The absence of old worker cells in the nest suggests two interesting possibilities. The colony may be in its second nest site. If so, then tropical bumble-bee colonies may not be as sedentary as is generally supposed, and may be able to move to a new site if the old one is destroyed. Or the colony may clear the nest of old worker cells before rearing a reproductive brood. This suggests that the usual method of determining a bumble-bee queen's productivity, counting the old worker cells, is not valid in the tropics. Having a mobile colony and cleaning

the nest site both would be of obvious value to bees nesting in an arboreal site. Finally, if the colony can readily move from, or clean out an old nest site, it is an easy step to become perennial rather than annual as are temperate zone bumble-bee colonies. All that would be required is increased longevity of the colony queen, or a system of queen supercedure. The young larvae in the nest suggest that this colony was beginning to rear another brood cohort after the maturation of this reproductive brood. There is no obvious ecological reason why this bumble-bee colony could not have continued to reproduce during the rainy season.

There were three wax moth larvae [*Galleria melonella* (L.)] feeding in the newly hatched cocoons. These scavengers may be responsible for the loss of some worker cells, but not their complete absence. Unidentified mites were abundant on the surface of the cells.

DISCUSSION

These brief observations suggest that the comparative rarity of lowland bumble-bees in the tropics may in part be due to the difficulties of nesting at or below ground level with the same degree of success as in temperate zones.

1) Moderately dry underground cavities are very rare in tropical forests during the rainy season.

2) Underground cavities are subject to frequent foraging by army ants (Dorylinae) as well as ants with stationary colonies; since the dry season is generally not severe enough to greatly depress ant populations, there is no time of year, such as the temperate zone spring, when the predatory threat is substantially reduced.

3) Predation by vertebrates in underground cavities or surface depressions is probably more intense in the wet tropical lowlands than in temperate areas. My observations agree with those of Sakagami et al. (1967): tropical *Bombus* are much more aggressive than temperate ones. This suggests that nest attack by large vertebrates is more frequent in tropical than temperate habitats. Coatis (*Nasua narica*), peccaries (*Tayassu* spp.), and pacas (*Cuniculus paca*) are likely nest predators; tame individuals of all three are very fond of honey, comb, and honeybee larvae.

As Sakagami et al. (1967) and Moure and Sakagami (1962) have emphasized, lowland tropical bumble-bee nests are usually found on the ground surface rather than in subterranean cavities. This behavior may alleviate the problem of flooding, but probably increases susceptibility to predation by ants and vertebrates. I feel that the next logical evolutionary step is to an arboreal nest site, and this has probably been more common than is generally realized, since such nests are difficult to locate. If Moure and Sakagami (1962) are correct in synonymizing *B. pullatus* with *B. atratus*, then the nest reported here is the second arboreal nest known for this bee. In addition, local residents at both

low and mid-elevation sites cannot locate nests of *B. pullatus* on the ground, but firmly believe that they often nest in trees. The aggressiveness of *B. pullatus* easily distinguishes it from all other tree-nesting large bees.

From the viewpoint of a large tropical social bee, arboreal nest sites are an improvement over sites on or in the ground, yet have some distinct disadvantages.

1) Since inclement weather (droughts, frosts, cold fronts, etc.) is much rarer in tropical forests than in temperate ones during the growing season, less insulation of the nest against the physical environment is needed to maintain a given internal nest temperature. This supposition is emphasized by the flimsy covering of dead leaves and light debris over surface tropical bumble-bee nests (Michener and LaBerge, 1954; Dias, 1958; Rau, 1941; Janzen, unpublished) and by the very thin walls of this *B. pullatus* nest. In short, as the physical environment becomes less severe, the suitability of arboreal nest sites increases, but ease of nest entry also increases for any animal that can brave the attack of the workers.

2) Elevated nest sites are drier. They are ventilated by drier air and usually well drained. The physical suitability of such sites for social bees is suggested by the fact that most tropical social bees nest in arboreal cavities or on arboreal surfaces. But by moving to arboreal sites, *Bombus* moves into competition with such cavity nesters as *Melipona*, *Trigona*, and *Eulaema* bees, and *Azteca* and *Crematogaster* ants. Except for *Eulaema*, these common Hymenoptera have large and long-lived colonies that, once established, probably cannot be chased out by *Bombus*. Further, these insects could probably evict a *Bombus* colony with little difficulty.

3) Arboreal sites such as the one described for *B. pullatus* are comparatively short-lived. The rapid turnover of arboreal nest sites may provide a marginal advantage to an annual species (such as *Bombus* generally appears to be) over other Hymenoptera having more permanent nests. However, the nest site is more likely to be destroyed once the colony is established. A *Bombus* colony will probably be more damaged by a fall than will an ant colony or a *Trigona* or *Melipona* colony, since *Bombus* does not relocate its brood and there is no reason to believe it would scavenge the remains of its own brood.

4) While an arboreal nest would be freer of predation by ants and vertebrates than a terrestrial nest, protection from ants still requires diligent guarding of the nest entrance. Incidentally, this can be done more efficiently by many small individuals than by the few large ones that guard a *Bombus* nest. *Trigona* and *Melipona* bees, and *Crematogaster* and *Azteca* ants, also make strong use of chemical defenses against intruders; the stings of a few large bumble-bees would be of little use against invading ants.

To a great extent, the success of any social insect colony depends on the profit per worker (the return to the colony for the cost of rearing

a single worker, Wilson, 1968). As the number of workers lost to predation increases, the profit per worker decreases. It becomes more difficult for the colony to establish itself and grow to reproductive size during the time afforded by an ephemeral nest site or a particular season. There are some indications that tropical bumble-bee workers are more heavily preyed on than are temperate ones. Rau (1941) cites 96% survival of worker *B. americanorum* (Fabr.) during an entire growing season in a Missouri colony, while two lowland Mexican nests of *B. medius* had already lost 31 and 25% of their workers by the middle of the growing season (about 3 months at both sites). If, in fact, the *B. pullatus* nest described here is perennial, and therefore more than a couple of years old, the losses to predation must be balancing the annual production rate of workers. This is a very different type of population regulation than may be operating in temperate areas, where Rau's (1941) example suggests that founding queen mortality regulates population density of colonies.

Worker bumble-bees appear to be far from the optimal size for a lowland tropical social bee. Being social, on an individual basis they are comparatively inept and stupid in predator avoidance (as are other social bees when compared with equal-sized solitary bees); selection has undoubtedly favored their harvesting ability in respect to colony growth over the ability of individuals to survive predation. Once located, a *B. pullatus* worker is the easiest caught of large bees in the lowland wet tropics (as compared with the solitary bees *Eulaema*, *Euplusia*, *Xylocopa*, and several Anthophoridae). She is a slow and clumsy flier, and slow to note rapid movements in her vicinity. Once caught, she is softer bodied and has a weaker sting than the other genera mentioned above. The loss of a tiny *Trigona* or *Melipona* worker to a predator is trivial compared to the loss of a single large *Bombus* worker, since there are few per nest. By having many small foragers, the *Trigona* or *Melipona* colony has many diverse foraging strategies available. By being large, alert, and well protected, the large solitary bees have high individual survivorship. *Bombus* appears to maximize neither advantage in the wet tropics.

Bumble-bees are distinctly more successful in lowland tropical areas with a severe dry season than in the wetter areas occupied by *B. pullatus*. Several species of black-and-yellow striped *Bombus* (e.g., *B. medius*) are locally common in lowland deciduous forest regions of Mexico and Central America. In the context of the earlier discussion, deciduous forest sites favor *Bombus* because 1) arboreal nest sites are poor for the other competing social bees owing to dry season desiccation, 2) the large solitary bees, being less versatile in their foraging behavior than *Bombus*, probably do less well with the fluctuating and erratic resources produced by a strong dry season, 3) ants and other potential *Bombus* predators fluctuate more in their density, and fewer species are present, 4) physically suitable terrestrial nest sites are probably more

abundant, and 5) an annual life cycle and periodic reproduction is better adapted to a seasonal than an aseasonal weather regime.

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LITERATURE CITED

- Bequaert, J. 1932a. Appendix to "Bees collected at Chichen Itza, Yucatan by the Harvard Expeditions of 1929-1930." Bull. Brooklyn Entomol. Soc. 27:17.
- . 1932b. An arboreal nest of *Bombus fervidus* (Fabricius). Bull. Brooklyn Entomol. Soc. 27:151.
- Dias, D. 1958. Contribuição para o conhecimento da bionomia de *Bombus incarum* Franklin da Amazonia. Rev. Brasil. Entomol. 8:1-20.
- . 1960. Notas sobre um ninho de *Bombus* construído acima do chão (Hymenoptera, Apidae). Rev. Brasil. Entomol. 9:151-156.
- Frison, T. H. 1930a. A contribution to the knowledge of the bionomics of *Bremus vagans* (F. Sm.) (Hymenoptera). Bull. Brooklyn Entomol. Soc. 25:109-122.
- . 1930b. A contribution to the knowledge of the bionomics of *Bremus americanorum* (Fabr.) (Hymenoptera). Ann. Entomol. Soc. Amer. 23:644-665.
- Gibson, A. 1930. Bumble-bee occupying oriole nest. Canadian Field-Naturalist 44:146.
- Howard, L. O. 1918. An unusual bumble bees' nest. Entomol. News 29:114-115.
- Janvier, H. 1955. Le nid et la nidification chez quelques abeilles des Andes tropicales. Ann. Sci. Nat. 11th ser. Zool. 17:311-349.
- Michener, C. D., and W. E. LaBerge. 1954. A large *Bombus* nest from Mexico. Psyche 61:63-67.
- Milliron, H. E. 1961. Notes on the nesting of *Bombus morio* (Swederus) (Hymenoptera, Apidae). Canadian Entomol. 93:1017-1019.
- Moure, J. S., and S. F. Sakagami. 1962. As mamangabas sociais do Brasil (*Bombus* Latreille) (Hymenoptera, Apoidea). Studia Entomol. 5:65-194.
- Myers, J. G. 1935. Ethological observations on the citrus bee, *Trigona silvestriana* Vachal, and other Neotropical bees. Trans. Roy. Entomol. Soc. London 83:131-142.
- Pitelka, F. A. 1954. Use of a bird nest by bumble-bee. Pan-Pac. Entomol. 30:220.
- Rau, T. 1941. The nesting habits of *Bombus medius* Cresson, the Mexican bumble-bee. Psyche 48:166-168.
- Sakagami, S. F., Y. Akahira, and R. Zucchi. 1967. Nest architecture and brood development in a Neotropical bumble-bee, *Bombus atratus*. Ins. Soc. 14:389-414.
- Sladen, F. W. L. 1912. The bumble-bee. Macmillan, London. 283 p.
- Wilson, E. O. 1968. The ergonomics of caste in the social insects. Amer. Natur. 102:41-66.