



Flight Ranges of *Melipona* and *Trigona* in Tropical Forest

Author(s): David W. Roubik and Martin Aluja

Source: *Journal of the Kansas Entomological Society*, Vol. 56, No. 2 (Apr., 1983), pp. 217-222

Published by: Kansas (Central States) Entomological Society

Stable URL: <https://www.jstor.org/stable/25084398>

Accessed: 11-06-2020 05:14 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



Kansas (Central States) Entomological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of the Kansas Entomological Society*

Flight Ranges of *Melipona* and *Trigona* in Tropical Forest

DAVID W. ROUBIK AND MARTIN ALUJA

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Panamá

ABSTRACT: Worker bees of *Trigona capitata* and *Melipona fasciata* were released at a range of distances from their nests in mature forest on Barro Colorado Island, Panamá. Prior to release, a small ferrous tag was glued on the thoracic notum, and this tag was removed from foragers returning to nests by a magnet, placed above the nest entrance. Maximum distances from which bees found their nests were near 2.1 km for *Melipona* and 1.5 km for *Trigona*, and regression analysis indicated probable maxima of 2.4 km and 1.7 km, respectively. The proportion of tagged foragers returning to the nest decreased arithmetically with increasing distance of release. This study provides the first information on maximum flight ranges of highly social bees within lowland tropical forest.

Data on flight ranges of stingless bees (Meliponinae) are of general interest to developing an understanding of tropical forest ecology. Stingless bees are tropical forest species, numbering at least 300 in the neotropics and 100 in the paleotropics. Their broad interaction with plants and animals (e.g., see Roubik, 1982a, b) make them one of the ecologically most diverse and important insect groups. The foraging range of a colony, genetic neighborhood size of plants pollinated by the bees and the potential distance between mother and daughter colonies all are functions of worker bees' flight range. No detailed study of such flight ranges has been made in mature forest with closed canopy. Accounts have been given of presumed or measured flight ranges of some species (Wille, 1965, 1976; Esch, Esch, and Kerr, 1965; Kerr, 1969; Bawa and Opler, 1975; Hubbell and Johnson, 1977; review by Michener, 1974). But this information is usually based on few observations, generally at artificial feeders or a species of flowering plant. The recorded flight ranges are not readily placed in perspective necessary to describe colony biology and the probability of foraging at a given distance from the nest.

Telemetry techniques developed for radio tracking of larger animals are not feasible for most insects. A novel approach devised by Gary (1971) was used to study foraging ranges of honey bees *Apis mellifera*, incorporating a magnetic mark-recapture system. We modified this technique to gauge flight distances of two stingless bees, *Melipona fasciata* Latreille and *Trigona* (*Cephalotrigona*) *capitata* Smith in the forest of Barro Colorado Island, Panamá. Our results show that flight ranges of these bees exceed that which had been postulated for meliponines.

Materials and Methods

Three study colonies of *M. fasciata* and two of *T. capitata* were located in tree cavities within old forest (250-300 years for the oldest trees) on Barro Colorado Island. Colonies of the former species consist of 400 to 800 adults and those of the latter generally have between 1000 and 1500 workers (Roubik, in prep.). The

size and anatomy of *Melipona* (Meliponini) differs markedly from that of most *Trigona* (Trigonini, Moure, 1951; Wille, 1979). *Melipona* resembles honey bees and its 40 species range from 6 to 15 mm in length, while *Trigona*, a far larger group with many distinctive supraspecific grades, ranges from 2 to 12 mm in length. Both species nest only in tree cavities, from 1–2 meters to over 20 meters above ground level, and are restricted to forest habitats.

Exiting foragers were captured at the nest entrance; a small ferrous tag was glued to the thoracic notum. Groups of tagged foragers were then transported a known distance from the nest and released, after they had fed on a honey-water saturated tissue placed in the vial in which they were kept. Prior to release of the bees, a 1 oz. horseshoe magnet was attached directly over the entrance of the nest. The nest entrance of both species is a hole only large enough for one bee to occupy. Metal tags were removed from returning bees by the magnet as they entered the nest. Each group of foragers released at a given distance carried tags marked in a distinctive way, to avoid confusion with bees released at other sites. Tags used for *M. fasciata* weighed 6 mg and were half circles 2.3 mm in diameter and 0.25 mm thick. The tags placed on *T. capitata* were of the same thickness but were $\frac{1}{4}$ circles weighing 3 mg. Tags were generously supplied by Dr. N. E. Gary and K. Lorenzen, University of California, Davis; details of their manufacture are given by Gary (1971).

Individual tags were applied only once to bees to avoid use of magnetized metal tags (i.e., those previously held by the magnet) which might interfere with geomagnetic orientation of foragers (Gould, 1980). The tag was attached with a small droplet of Elmer's Glue-all while the bee was held with the fingers. At least 20 minutes was allowed for the glue to harden prior to the bee's release. Tags which were not well placed and cemented on bees became detached within this time. Tags recaptured by the magnets were usually collected on the day following release of tagged foragers in the forest. This portion of the methodology was important both in allowing time for a released bee to return and for a tag to be recaptured by the magnet. Bees carrying ferrous tags were usually unable to pass by the magnet; even if a bee was capable of pulling away from the magnet with a tag still in place, later exits from the nest resulted in tag recapture. In addition, we noted repeatedly that nest mates attempted to remove tags from foragers and discard them from the nest. Thus, if a tag arrived on a bee, it appeared certain that it would eventually be recaptured by the magnet, from which it could not be separated by the bees.

Bees were transported to the release site in a plastic vial 10 × 3 cm in diameter. Release sites were chosen at positions next to trail markers on Barro Colorado Island. The sites included distances from less than 500 meters to greater than 2000 meters from nests, spreading 360° from the nest site (Fig. 1). All bees that flew directly out of vials, made circling flights around the release site, then flew to the canopy were scored as successful releases. Bees which did not fly after release were not used in the study. A total of 427 bees were tagged, 167 *T. capitata* and 260 *M. fasciata*. Per nest, the number tagged was 100 and 67 for the former species, and 105, 128 and 27 for the latter; 93% of tagged bees were successfully released. Release of tagged bees took place between 1015 and 1445, local time. We conducted the experiments during the late wet season of 1981, from October until December.

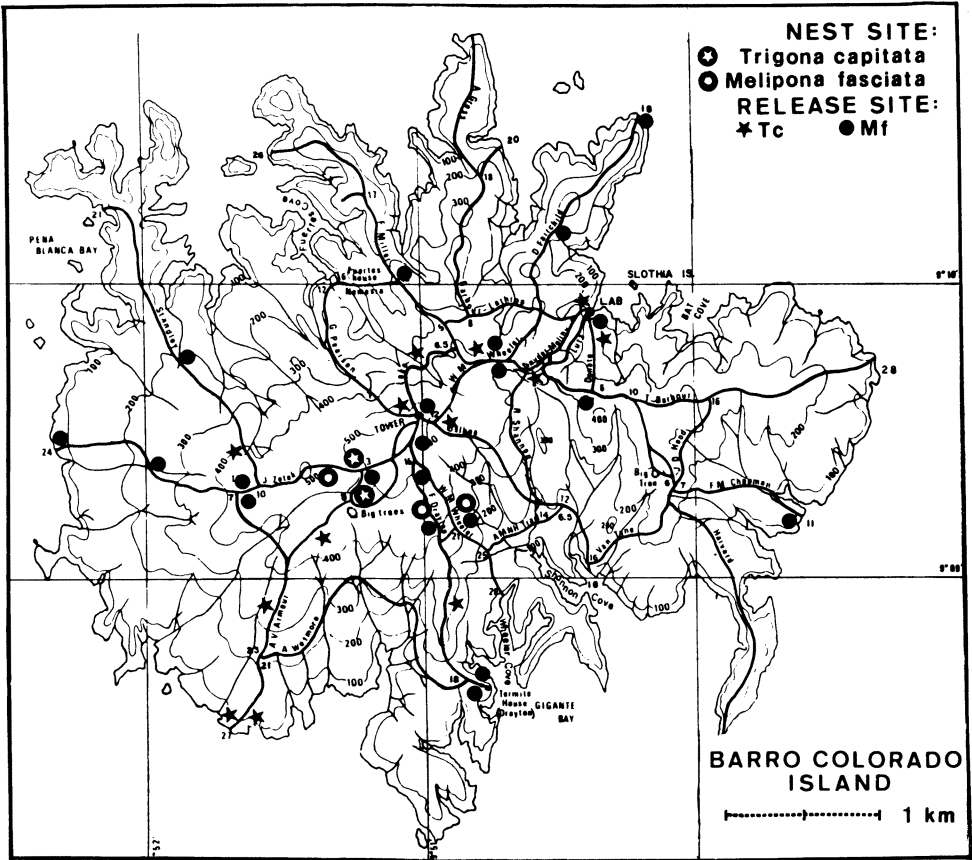


Fig. 1. Map of the study site, Barro Colorado Island, within Barro Colorado Nature Monument (Smithsonian Tropical Research Institute) in central Panamá. Nest localities of *Trigona capitata* and *Melipona fasciata* and sites at which tagged foragers were released are indicated on the map.

Results

The proportion of tagged foragers returning to the nest from release sites is plotted in Fig. 2. Foragers of *M. fasciata* returned from distances of 155 to 2085 meters. *Trigona capitata* returned from 505 to 1547 meters. Of 228 *M. fasciata* successfully released, 45 arrived at the nest. For *T. capitata*, 167 were released and 16 arrived. The probability of return for each species decreased arithmetically with increasing distance from the nest. The lines plotted in Fig. 2 adequately represent this relationship ($P = 0.04$ and $P < 0.001$, *T. capitata* and *M. fasciata*, respectively). Addition of exponential terms in the linear equations did not produce a better statistical fit to the data points. The release points from which no foragers returned to the nest were excluded in the regression analysis, since any number of points beyond the flight range of bees could be included, which would distort the relationship between distance and probability of return.

The proportional return success of foragers of each species was calculated by considering the total number of bees released at sites from which at least 1 bee in the group returned to the nest (group size did not exceed 15 and was usually

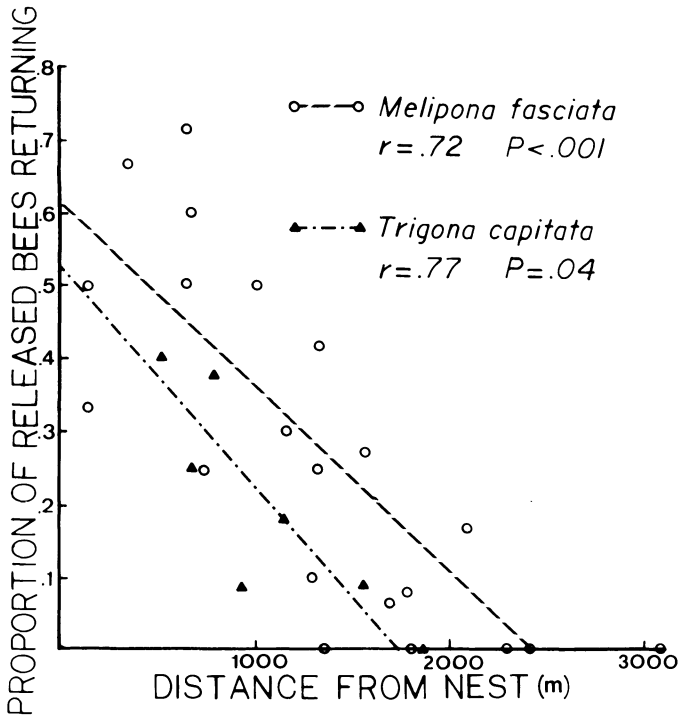


Fig. 2. Plotted proportions of released foragers returning to their nests from a range of distances, and linear regression lines fitted to the points. Distances from which no released bees returned to their nests were excluded in regression analysis.

12 bees). *T. capitata* successfully located its nests in 16 of 84 such releases (0.19) and *M. fasciata* did so with a probability of 45/144 (0.31).

Regression lines plotted in Fig. 2 give probable maximum flight ranges for the two species, or the maximum distance at which bees would be expected to return to nests. The expected maximum for *T. capitata* was 1.65 km and that of *M. fasciata* was 2.4 km.

Discussion

The foraging activity of *M. fasciata* and other meliponines does not appear to vary significantly during the year on Barro Colorado Island, nor does the number of different flower species visited for pollen (Roubik et al., in prep.). Despite notable differences in the number of plant species flowering during distinct seasons in this habitat (Croat, 1978), it is conceivable that average foraging ranges of bees studied here do not vary seasonally. Our data indicate maximum *flight* ranges of the bees and the foraging patterns of colonies in mature lowland forest. These data need not be equivalent to maximum *foraging* ranges, even though we fed tagged foragers prior to release.

It is possible that a bee released beyond its previous flight range enters familiar territory (that in the direction of the nest) by chance. Graphical analysis of this phenomenon, however, revealed that the chance of flying in the right direction

when released beyond flight range is small, and that of reaching the nest is in most cases insignificant. Slightly beyond the maximum distance at which a forager possesses orientation sufficient to return to the nest, the probability of flying in the right direction by chance is close to 0.5. At a distance of 1.2 times the maximum orientation range, this probability decreases to 0.3; at 2 times the range it is 0.17. At three times the orientation radius from the nest, the chance of flying to some portion of the area familiar to the bee is about 0.1. The preceding computations were made by determining the angle subtended by two lines drawn tangential to a circle from point at a given distance from the edge of the circle. The proportion of 360° (the total flight directions a bee might take) constituted by such an angle is the probability of intersection with a known area (the circle) by chance. This analysis does not take into consideration the forager's ability to fly the distance to its previous orientation range. Thus the actual probability of return to the nest by chance is substantially lower than that given by the above computations. This argument, we believe, supports the inference of maximum flight range from our experimental results. However, further extrapolations from these data should be made cautiously. For example, for *T. spinipes* in southern Brasil, Kerr and co-workers (W. E. Kerr, pers. comm.) have shown that the foraging range of a colony is not equivalent to the range at which workers will prepare a new nest site for colony reproduction. Pollinator effectiveness also depends on the number of plants or flowers visited, regardless of distance from the nest, and the efficiency of pollinators cannot be surmised from their flight ranges.

In addition, it is apparent from our data that the behavior of workers released at moderate distances from the nest is dependent on directional orientation. Fig. 2 indicates an expected probability of return ranging from 0.5–0.6 for bees released at the nest site, which is probably due to our selection of minimum distances for bee release. Bees navigate to and from their nest by using combined information from landmarks, the position of the sun, planes of polarized light, airborne odors, geomagnetic fields and perhaps other cues (Michener, 1974; Gould, 1980; Rosin, 1978). At some distance from the nest, apparently less than a few hundred meters, site orientation of a forager may differ considerably in different directions. A forager visiting flowers 300 meters E of the nest may not recognize orientation cues if released 300 meters W of the nest. No tagged foragers of *T. capitata* were released at less than 500 meters from their nests, and only 3 of 20 releases for *M. fasciata* were at such short distances (Fig. 2). This inherent bias in the data led to the apparent underestimate of the probability of forager return indicated in Fig. 2, although in five releases of *M. fasciata* from less than 1000 meters from the nest, from 0.5 to 0.71 of the released foragers returned. Our data do suggest that at intermediate distances, forager orientation is indeed influenced by direction from the nest. If at moderate distances from the nest foragers maintain orientation within 180° of their flight path, then the average probability of return within a population of foragers released at random points would be 0.5. This calculation, as in the preceding discussion, also assumes that all foragers are physically able to fly as far as the nest, which seems reasonable at shorter distances. In conclusion, the probability of return indicated by regression analysis is consistent with flight and directional orientation capability at intermediate distances from the nest, but does not adequately represent these variables at lesser distances.

The directional component of forager orientation implies that maximum flight

range may exceed the distances recorded in this study. Had we tagged and released all foragers of the study colonies, the recorded maxima would probably be expanded, and regression analysis might have shown a logarithmic relationship, or Poisson distribution of probability of return as a function of distance from the nest. Within the normal flight and orientation ranges of the bees, however, this relationship was arithmetic. It is also of interest that *T. capitata* uses pheromone trails at times during foraging (Michener, 1974), but released foragers returned with a probability not differing greatly from that for *M. fasciata*, which does not forage with odor trails. While our study does not show maximum flight ranges in every conceivable situation, it does emphasize the normal flight capabilities of foraging *Melipona* and large *Trigona* in a tropical forest.

Acknowledgments

We thank the EXXON Corporation for a research assistantship granted to M. Aluja and the Smithsonian Institution for Scholarly Studies grant 1234S102 to the senior author.

Literature Cited

- Bawa, K. S., and P. A. Opler. 1975. Dioecism in tropical forest trees. *Evolution* 29:167-179.
- Croat, T. C. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Palo Alto, California, 943 pp.
- Esch, H., I. Esch, and W. E. Kerr. 1965. Sound: an element common to communication of stingless bees and to dances of honey bees. *Science* 149:320-321.
- Gary, N. E. 1971. Magnetic retrieval of ferrous labels in a capture-recapture system for honey bees and other insects. *J. Econ. Entomol.* 64:961-965.
- Gould, J. L. 1980. The case for magnetic sensitivity in birds and bees (such as it is). *Amer. Sci.* 68: 256-267.
- Hubbell, S. P., and L. K. Johnson. 1977. Competition and nest spacing in a tropical stingless bee community. *Ecology* 58:949-963.
- Kerr, W. E. 1969. Some aspects of the evolution of social bees. *Evol. Biol.* 3:119-175.
- Michener, C. D. 1974. *The Social Behavior of the Bees*. Harvard Univ. Press, Cambridge, Mass. 404 pp.
- Moure, J. S. 1951. Notas sobre Meliponinae. *Dusenía, Curitiba* 2:25-70.
- Rosin, R. 1978. The honey bee "language" controversy. *J. Theor. Biol.* 72:589-602.
- Roubik, D. W. 1982a. The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology* 63:354-360.
- . 1982b. Obligate necrophagy in a social bee. *Science* 217:1059-1060.
- Wille, A. 1965. Las abejas atarrá de la región mesoamericana del género y subgenera *Trigona*. *Rev. Biol. Trop.* 13:271-291.
- . 1976. Las abejas jicótes del género *Melipona* de Costa Rica. *Rev. Biol. Trop.* 24:123-147.
- . 1979. Phylogeny and relationships among the genera and subgenera of the stingless bees (Meliponinae) of the world. *Rev. Biol. Trop.* 27:241-277.