

# POPULATION DENSITIES AND BIOMASS OF NEOTROPICAL SOCIAL WASPS (HYMENOPTERA, VESPIDAE) RELATED TO COLONY SIZE, HUNTING RANGE AND WASP SIZE

Anthony Raw<sup>1</sup>

**ABSTRACT.** At a locality near Brasilia the sizes of hunting areas and of colonies of 13 species of social wasps varied greatly. Size of the hunting area varied 152 fold and was strongly related to the number of adult wasps per colony which varied 400 fold. The total number of adults of the 13 species was estimated at 182.9/ ha (range 7.1 fold among the species) and their total biomass was 1.6 kg/ ha (range 3.6 fold). Hunting range was not significantly related to body size. Variation in wing area (11.3 fold) was similar to that of the fresh weight of the adult female (10.7 fold). Eleven species showed habitat preferences where they hunted. Models relating prey size to the distance prey are carried are discussed.

**KEY WORDS.** Vespidae, colony size, densities, hunting area, neotropics

Social wasps of the family Vespidae are ubiquitous members of lowland neotropical ecosystems. In Central Brazil, as elsewhere in the country, several species occur together (RAW 1988, 1998). Most of the neotropical species of social wasps whose diets are known hunt arthropods and many are foliage gleaners (GOBBI & MACHADO 1985, 1986; RAVERET-RICHTER & JEANNE 1985; MACHADO *et al.* 1987; MACHADO *et al.* 1988; RAW 1988, in press; RAVERET-RICHTER 1990; MONTILLOR & BERNAYS 1993). The most obvious differences among the coexisting species are the sizes of the adults and of their colonies and it was suspected that these two characteristics might influence their population densities.

Social wasps lend themselves very well to studies on populations ecology. The relative ease of locating the nests of most species and the strong aggregations when the wasps are at their nests make the task of counting their populations far easier than in solitary animals. Counts of nest populations are more reliable than estimates of the numbers of wasps away from their nests where many individuals can be overlooked.

However, without information on the wasps' hunting ranges, the densities of wasps which might be implied from their colony densities can be misleading. For the present investigation the potential areas tapped by colonies were considered to be circular, though the shape can be expected to vary temporarily with the fluctuating availability of resources. The numbers and sizes of wasp colonies, the body sizes of adult female wasps and their hunting ranges were examined.

1) Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz. Rodovia Ilhéus - Itabuna Km 16. 70910-900 Ilhéus, Bahia, Brasil.

## Study area

At a locality in the Cabeça de Veado valley, 12 km south of the centre of Brasília (15°52'S, 47°52'W), several species of social wasps hunted together. The total area surveyed was 15 ha (500 m X 300 m) which comprised the 4 ha (400 m X 100 m) study site and a border 1 ha wide along each side and 0.5 ha beyond each end. The 4 ha study site was a garden bordered on three sides by natural vegetation typical of the region. The western boundary of 400 m was the edge of evergreen, riparian forest along a permanent stream while to the south and east there was "campo limpo" and "campo sujo". These are forms of open cerrado; the savanna-like vegetation typical of Central Brazil described by EITEN (1972). A house was situated in the south-west corner of the study area and to the north were neighbouring gardens.

The garden where the study was conducted contained numerous native and exotic tropical trees and shrubs. There were also annual fruit, vegetable and many ornamental plants interspersed with lawns. The native trees included *Byrsonima umbellata* A.Juss. (Malpighiaceae), *Cassia ferruginea* (Schrad.) Schrad. ex DC. (Leguminosae), *Jacaranda cuspidifolia* Mart. and *Tabebuia impetiginosa* (Mart.) Standl. (Bignoniaceae) and *Tapirira guianensis* Aubl. (Anacardiaceae).

## METHODS

In order to estimate the total numbers of social wasps in the study area, their colonies were located and the number of occupants in the smaller nests were counted and, in the larger nests, were estimated. Species of *Polistes* Latreille, 1802 and *Mischocyttarus* de Saussure, 1863 construct open nests with a single exposed comb on which all the wasps are visible. The numbers of adult female wasps on each of the nests of this type were counted between 06.00 hr and 06.40 hr before the wasps became active. Males are common in medium-sized and large colonies of *Mischocyttarus*, but are easily distinguished from the females. The nests of the other species studied are totally enclosed in a paper outer wall so nests were collected in order to count the number of adult occupants. The large colony of *Polybia ignobilis* (Haliday, 1836) was inaccessible so the colony size was estimated based on counts of three colonies of similar size located 8, 19 and 23 km from the study area.

In February, 1987 the total area of 15 ha was searched during 16 hours for wasps and their nests. During the following six weeks the 4 ha study site was searched two hours per day, three days per week for hunting wasps. On each occasion that a wasp was seen its exact location in the garden was noted and the distance from the wasp to the nearest nest of that species was measured to within 1 m for ten of the species and within 5 m for *Synoeca surinama* (Linnaeus, 1767) and 10 m for *P. ignobilis* and *Epipona tatusa* (Cuvier, 1797).

The hunting ranges were measured in order to compare the areas used by the colonies. The mean of the 25 longest distances from the nest (of the 30 to 42 recorded) for each species was used as the radius of the circle (here called the hunting range) of the area utilized for hunting and foraging. Each time a wasp was located the vegetation type of the place was also recorded. The vegetation was categorized



simply as either open areas without trees (lawn, flower beds and vegetable plots) or under trees which were 4 m to 6 m tall. At the boundary between the two vegetation types the wasps which were encountered in sunny locations were considered to be in open areas and those in shade under trees.

Twenty adult females of each species were starved for three or four hours and then weighed to  $10^{-4}$  g and the lengths of their fore-wings measured to  $10^{-4}$  m. Only eight females of *Mischocyttarus goyanus* Zikán, 1949 were measured. The biomass of adults per hectare for each species was calculated using the data on fresh starved body weight and the estimated densities of wasps in the study area.

## RESULTS

### Numbers of colonies

Thirteen species of social wasps hunted in the study area of 4 ha (Tab. I). Twenty nine active colonies of ten species were discovered in the area. Those of *Mischocyttarus cerberus* Ducke, 1918, *M. cassununga* (von Ihering, 1903), *M. goyanus*, *Polistes satan* Bequaert, 1940 and *Parachartergus fraternus* (Gribodo, 1892) were attached to the roof and window frames of the house. Nests of *Pseudopolybia vespiceps* (de Saussure, 1864), *Polybia fastidiosuscula* de Saussure, 1854, *P. occidentalis* (Olivier, 1791), *P. paulista* von Ihering, 1896 and *Brachygastra augusti* (de Saussure, 1854) were suspended from the branches of trees. The colonies of *Polybia paulista*, *P. occidentalis*, *Parachartergus fraternus* and *Brachygastra augusti* were located near the corners of the study area. The three other species that hunted in the study area had established colonies outside the garden. The nest of *E. tatua* was suspended from a branch at the forest edge 90 m from the edge of the study area. The nest of *S. surinama* was 50 m and that of *P. ignobilis* was 150 m distant in the forest. The first was affixed to a tree trunk and the second was located inside a hollow tree.

In the survey of the entire 25 ha plot a total of 23 species was located. These included one colony each of *Synoecca surinama*, *E. tatua* and *P. ignobilis* whose members hunted in the study site. Of the 10 species which nested in the 4 ha plot colonies of only *M. cerberus*, *Polistes satan* and *Polybia occidentalis* were found in the surrounding area with respectively eight, two and one colonies.

### Densities of wasp populations

In some instances, the nests of different species were located close together. The closest nests of four of the five species that nested on the house (three species of *Mischocyttarus* and *Polistes satan*) were only 20 cm to 5 m apart. The nests of *Polybia occidentalis* and *B. augusti* were 2 m apart in a *Cassia* tree 100 m from the house, a large nest of *P. paulista* was located in a *Schizolobium parahyba* (Vell.) Blake tree 25 m distant and a nest of *Ps. vespiceps* in an unidentified tree 40 m distant. The nest of *P. fastidiosuscula* was suspended from the branch of an unidentified tree 25 m from the house. Dividing the study area into four 1-ha plots, 25 colonies were located within one of the plots which contained the house and 4 were in a second plot, whereas colonies were not found in two plots.

The numbers of adult wasps of the 13 species in the 4 ha study area ranged from 12.7 to 90.7 (Tab. I), so the density of the most abundant species was 7.1 times greater than the rarest one. The hunting areas of ten of the species extended beyond the limits of the study area and the number of active wasps of these was calculated to be 575.6, while the number of wasps of the three species with smaller colonies whose hunting areas were entirely contained within the study area totalled 156 (Tab. I). Thus the number of adult female wasps that occupied the study area of 4 ha was estimated to be 731.6 which gives a mean of 182.9 adult wasps / ha. The number of adult female wasps per colony varied from 5 to 2,000 among the species; a 400 fold difference (Tab. II). Colony size was strongly correlated with the size of the hunting area ( $r^2 = 0.948$ ,  $P < 0.00001$ ; figure 1).

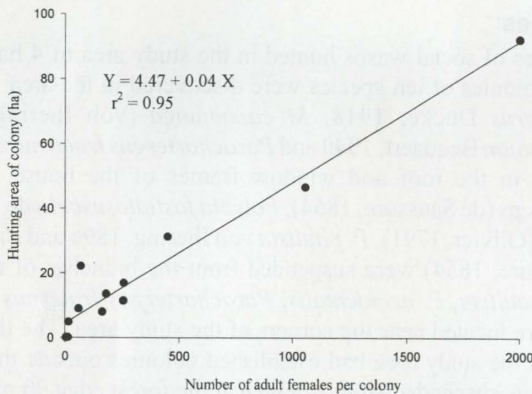


Fig. 1. The relationships of colony size to hunting area in 13 species of social wasps at a locality near Brasilia.

Table I. The sizes of colonies and hunting areas, densities and biomass of 13 species of social wasps in an area of four hectares near Brasilia. The colonies of three species (marked \*) were outside the study area.

Species	Number of colonies in study area	Mean number of adults females per colony	Hunting area per colony (ha)	Number of adult females in study area (4ha)	Mean fresh starved weight per wasp (mg)	Biomass (fresh weight in mg) of wasps in study area (4ha)
<i>M. cerberus</i>	10	5	0.06	50.0	23.5	1175.0
<i>M. goyanus</i>	4	7	0.07	28.0	47.5	1330.0
<i>M. cassununga</i>	6	13	0.10	78.0	28.7	2238.6
<i>P. satan</i>	3	16	4.91	13.0	157.2	2048.7
<i>P. vespiceps</i>	1	60	8.98	26.7	46.0	1229.9
<i>S. surinama</i>	*	70	22.10	12.7	147.2	1867.5
<i>P. fastidiosuscula</i>	1	164	8.00	82.6	14.7	1213.7
<i>B. augusti</i>	1	181	13.50	53.8	32.1	1725.8
<i>P. fraternus</i>	1	257	11.40	90.6	36.4	3298.1
<i>P. occidentalis</i>	1	259	16.90	61.2	16.2	992.1
<i>E. tataua</i>	*	450	31.20	57.7	53.3	3076.5
<i>P. paulista</i>	1	1056	46.60	90.7	21.3	1931.3
<i>P. ignobilis</i>	*	2000	92.30	86.6	41.6	3604.6



Table II. Summary of ranges of values of various measurements of 13 species of social wasps hunted at a locality near Brasilia.

	Range	Difference factor
Biomass (weight of adults- g/ ha)	0.29 – 0.90	3.1
Population density	20.20 – 90.7	7.1
Length of forewing (mm)	6.40 – 21.5	3.4
Body weight (mg)	14.70 – 157.2	10.7
Hunting area (ha)	0.06 – 92.3	154.0
Colony size (number of adults)	5.00 – 2000.0	400.0

### Sizes of adult wasps and biomass

The mean lengths of the fore-wings varied 3.4 fold (6.4 mm to 21.5 mm) from the shortest to the longest species studied, while the range of the fresh starved body weight varied by a factor of 10.7 (Tab. II). The total biomass (fresh starved weight of adult female wasps) of the 13 species in the 4 ha study was 25.7 g; equivalent to 6.4 g/ha (Tab. I). The biomass varied by a factor of 3.1 among the species. The lowest was *P. occidentalis*, followed by *P. fastidiosuscula*, and the highest was *P. ignobilis*.

### Hunting ranges

A total of 443 distances was measured from where wasps were encountered to their nests. The total number of measurements per species ranged from 30 to 42. The mean hunting ranges varied twelve fold, from 44 m to 542 m among the species. The correlation of the hunting range with length of the fore-wing of the 13 species was not significant ( $r^2 = -0.102$ ,  $P = 0.740$ ).

Hunting areas were calculated from the above distances. They varied from 0.6 ha to 92.3 ha (a 152 fold range) (Tab. I). The sizes of the hunting areas could be conveniently placed in two categories and one species was intermediate. The total areas used for hunting by the three species with the shortest hunting ranges (the three *Mischocyttarus* species) were contained entirely within the garden and covered 15%, 18% and 24% of the study area. The nests of the three *Mischocyttarus* species and *P. satan* were built very close together and consequently the colonies' hunting areas overlapped. The 4 ha area comprised only part (4% to 50%) of the estimated hunting area of the nine remaining species and, in particular it comprised only small parts (4%, 13% and 18%) of the hunting areas of the three species with the longest hunting ranges and whose nests were located further afield. *P. satan* is intermediate and the garden comprised 81% of its hunting area. These hunting areas were used to calculate the densities of the populations of the 13 species (Tab. I).

### Habitat use

The vegetation cover of the study area is heterogeneous, encompassing areas of trees and open vegetation and included patches where some species hunted and others where they did not. The 13 species hunted over many types of plants and their hunting areas overlapped partially or totally. However, 11 of the species showed significant preferences between open and shaded vegetation (Tab. III, Chi-square test). Most individuals of the three *Mischocyttarus* species, *S. surinama*,

*Polybia fastidiosuscula* and *Parachartergus fraternus* were found in shade under trees. In contrast *Polistes satan*, *Polybia occidentalis*, *P. paulista*, *B. augusti* and *E. tatus* were seen more often in more open places on the arable crops and flower beds. Approximately 70% of the study area was in full sun at mid-day. Only *P. ignobilis* and *Polistes satan* were seen hunting on the lawn.

Table III. The utilization of open and shaded vegetation by 13 species of social wasps hunted at a locality near Brasilia.

Species	Number of observations	Number (and percentage) in open locations	Value of P (Chi-square)
<i>Mischocyttarus cerberus</i>	66	4 (6)	<0.001
<i>Synoeca surinama</i>	45	7 (16)	<0.01
<i>Mischocyttarus cassununga</i>	54	5 (9)	<0.001
<i>Polybia fastidiosuscula</i>	72	8 (11)	<0.001
<i>Parachartergus fraternus</i>	60	13 (22)	<0.01
<i>Mischocyttarus goyanus</i>	41	11 (27)	<0.05
<i>Pseudopolybia vespiceps</i>	37	13 (35)	NS
<i>Polybia ignobilis</i>	89	54 (61)	NS
<i>Polybia paulista</i>	94	66 (70)	<0.01
<i>Polistes satan</i>	68	62 (91)	<0.01
<i>Polybia occidentalis</i>	61	57 (93)	<0.001
<i>Brachygastra augusti</i>	54	54 (100)	<0.001
<i>Epipona tatus</i>	35	35 (100)	<0.001

(NS) Not significant at the 5% level.

## DISCUSSION

The wasps were counted or their numbers estimated at their nests in the present investigation so the data on population sizes are considered to be more accurate than counts of wasps when they are hunting and foraging. Often it is difficult to locate individual wasps in dense vegetation and in tree tops and many are overlooked. The estimates of hunting range of nine of the species are also considered to be relatively accurate. However, the mean hunting ranges of four were > 240 m and they might have been under estimated in a study area 400 m long. The wasps are the three whose colonies were located outside the study area and *Polybia paulista* whose nest was located near one end of the study area. Nonetheless, no additional colonies of these four species were encountered in the 25 ha plot; the only ones being those cited in table I.

As seen in the present investigation, very often relatively large colonies are encountered close together due to the limited availability of nest sites. More than half the study area contained no colony – possibly through a lack of suitable nest sites. Likewise, DINIZ & KITAYAMA (1994) recorded eight colonies of six species of *Polybia* in a single hectare of gallery forest in Mato Grosso state also in Central Brazil.

During the present study, quantitative information was not collected on the levels of predation. However, a larger colony is said to furnish the advantage of a high of survivorship of its occupants. In particular, larger colonies may suffer fewer attacks and be able to re-establish themselves more quickly than smaller ones (JEANNE 1975, 1980).



The hunting areas of the 13 species overlapped partially or totally. However, a factor believed to be important in niche separation is the significant preferences which the species demonstrated between the two types of habitat where they hunted. Eleven of them could be classified as either forest or open area species according to the type of habitat in which they hunted in natural vegetation and in equivalent vegetation types in the garden. The neotropical social wasps which have been investigated restrict their hunting to broad habitat types (RAW 1992, 1998). Several species nest in the forest and hunt in adjacent open areas (RAW 1988).

The biomass and population densities of the adult females of all 13 species in the study area were relatively low (varying by factors of 3 and 7) and the two factors expressing body size were similar. In marked contrast, the ranges of measurements of hunting range and colony size were very large (154 and 400 fold). The strong correlation between hunting range and colony size demonstrates that the members of a larger colony hunt over a wider area in their search for the resources which the colony requires.

The rich social wasp fauna of the Cabeça de Veado valley may be explained partly by the location of the study area being at the margin of the forest. The forest edge is a rich habitat in tropical Brazil with a greater diversity and abundance of social wasps than either forest or open savanna (RAW 1992, 1998) which may account for the high density of wasps in the study area compared with nearby areas of open savanna (HENRIQUES *et al.* 1992).

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