THE THIRD TROPHIC LEVEL OF PLANT DEFENCE: NEOTROPICAL SOCIAL WASPS' USE OF ODOURS OF FRESHLY DAMAGED LEAVES WHEN HUNTING

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ABSTRACT. An important aspect of the hunting strategy of neotropical social wasps (Hymenoptera: Vespidae) is where they hunt. Three species used two behavioural components in their selection of a place to search for prey. The wasps utilized the odour of freshly damaged leaves as cues (which could be synomones) to select which leaves to inspect and also they remembered a place to which they were strongly attracted to hunt recently and returned there. *Polybia ignobilis* (Haliday, 1836) and *Polistes satan* Bequaert, 1940 hunted on a lawn of *Digitaria diversinervis* Stapf immediately after it was mown in significantly larger numbers than at other times. *P. ignobilis* and *Polistes versicolor* (Olivier, 1791) hunted in significantly greater numbers on freshly cut leaves of passion vine (*Passiflora edulis* Sims) than on uncut leaves. Sometimes wasps inspected cards rubbed with freshly crushed leaves of *P. edulis*, but not control cards. Preliminary data suggest that several other species of social wasps around Brasília hunt in a similar manner on native and exotic plants. Apparently the production of ephemeral odours by freshly cut leaves attract generalist insectivorous predators which perceive these scents and the social wasps investigated are members of the third trophic level of the plants' defence against attacks by herbivores. Available information suggests a difference between the behaviour of generalists and that of specialist arthropod predators which are attracted to the odour emitted after their particular prey have damaged the leaves.

KEY WORDS. *Polybia*, *Polistes*, wasps, plant defence, neotropics

Over the past two decades there has been a growing realization of the importance of arthropod predators in the plant's defence system against the attacks of herbivorous insects and PRICE *et al.* (1980) argued that "The third trophic level must be considered as part of a plant's battery of defences against herbivores." PRICE (1986) further suggested that plants have adapted the use of these predators to become part of their defence strategy. It has been known for some time that injury to a plant by a herbivore can release particular odours (*e.g.* MONTEITH 1955, VARLEY & GRADWELL 1958) and that the predators of these herbivores can be attracted to the odour at the site of damage (HASSELL 1968; VINSON 1975).

In most neotropical, terrestrial communities the animals commonly involved at the second trophic level are herbivorous insects and the members of the third trophic level are insectivorous insects, birds and lizards. It has been suggested that the involvement of arthropod predators in this defence strategy differs somewhat from that of vertebrate predators because of the formers' very sensitive olfactory senses. The hunting strategy of some arthropods is said to function through their

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perception of leaf damage (VINSON 1976; PRICE *et al.* 1980). More specifically it has been demonstrated that substances are released through foliar damage and these provide predators and parasitoids with olfactory cues about the presence of prey (ODELL & GODWIN 1984, FAETH 1985) and are called herbivore-induced plant volatiles (TAKABAYASHI & DICKE 1997). Investigations on the subject to date have been conducted under laboratory conditions on parasitoid wasps, bugs, beetles, flies and mites (HASSELL 1968; VINSON 1976; REID & LAMPMAN 1989; DICKE *et al.* 1990; TURLINGS *et al.* 1990; TAKABAYASHI & DICKE 1997).

Social wasps (Hymenoptera: Vespidae) comprise an important group of predators on herbivorous insects. They are widespread, though neotropical species are relatively restricted in the habitats where they nest and hunt (RAW 1988, 1992, 1998a). They are also common in many habitats. For example, during a complementary investigation in one of the study areas (Cabeça de Veado) the density was estimated at 183 adult social wasps per hectare (RAW 1998b). Nonetheless, little relatively has been written on social wasps' general hunting strategies or their specific behaviour when hunting. The published evidence suggests that social wasps hunt individually and use sight, scent and taste to locate their prey (JEANNE 1972; RAVERET-RICHTER & JEANNE 1985). Furthermore, individuals learn where they hunted successfully and return to those sites (RAVERET-RICHTER 1990; RAVERET-RICHTER & JEANNE 1985).

An important question on their food gathering is whether social wasps might communicate the location of a resource as the members of ant and bee colonies do (WILSON 1971). The major protein sources of many social wasps are caterpillars and other soft-bodied insects (GOBBI *et al.* 1984, GOBBI & MACHADO 1985, 1986; MACHADO & GOBBI 1987; MACHADO *et al.* 1987, MACHADO *et al.* 1988, RAW 1988; RAVERET-RICHTER 1990; MONTILLOR & BERNAYS 1993) and often this resource is not aggregated, in which case the discovery of one prey item does not necessarily indicate the presence of others at the same site. The need to search for widely dispersed prey might inhibit the use of a system of communication among wasps to recruit their sisters to a resource. At any rate, there is no evidence for a nest-based mechanism for recruitment to a site where a prey item was captured. In one species subject to a detailed investigation the wasps did not enlist their sisters to the site (JEANNE *et al.* 1995). This is in marked contrast to the behaviour of social bees, termites and most ants which very often forage at highly concentrated resource patches and recruit their sisters to the resource (WILSON 1971; CARROLL & JANZEN 1973; FRANKIE *et al.* 1976, O'TOOLE & RAW 1991).

Notwithstanding this presumed limitation among social wasps, several species possess efficient systems of communication among their siblings for other purposes. Two examples are the use of alarm pheromones by *Apoica pallens* (Fabricius, 1804), *Polybia paulista* von Ihering, 1896, *P. sericea* (Olivier, 1791), *Protonectarina sylveirae* (de Saussure, 1854) and *Synoeca surinama* (Linnaeus, 1767) to advise sisters of an attack on the nest (personal observation) and the scent-marking along a route which a swarm follows to a new nest site; a method employed by members of several genera (JEANNE 1975; NAUMANN 1975; WEST-EBERHARD 1983) including *S. surinama* and *P. sericea* (personal observation).

Outside the nest, social wasps spend much of their time searching foliage for prey and there is no doubt about their hunting efficiency. For example, a major difficulty in one investigation which involved identification of the prey was to find caterpillars before the wasps did (RAW 1988). Nonetheless, for the individual wasp, the area where she hunts contains an enormous volume of vegetation. Therefore, the question is, when a wasp leaves the nest on a hunting foray, does she fly to any plant at random to start her search or has she a strategy ? This study addressed one particular question of the individual wasp's hunting behaviour. Where will a wasp hunt?

My field observations suggested that several species of social wasps might use the odour of freshly damaged leaves to indicate the possible presence of their prey in addition to using visual and chemical recognition of the actual prey. Experiments were conducted on two plant species. In one the numbers of wasps which hunted on a recently mown lawn were recorded. However, the investigator's presence and the small size of the leaves of the grass made close inspection of the wasps' behaviour on the lawn difficult. Therefore, passion vine (*Passiflora edulis* Sims) was chosen for a second experiment. The wasps often hunted among the leaves of *P. edulis*, the plants are common and the trilobate leaves are large; the overall measurements of most were about 8 cm long x 10 cm wide.

Organisms and study areas

The behaviour of three species was investigated in detail around Brasília (15°S, 48°W). *Polybia ignobilis* (Haliday, 1836), *Polistes satan* Bequaert, 1940 and *P. versicolor* (Olivier, 1791) hunted on passion vine and the two former species also hunted on a lawn immediately after it was mown. Corroborative notes were collected on eight other species which hunted on native and exotic plants.

The study was conducted in ten suburban gardens within a radius of 16 km of the centre of Brasília and on one farm 34 km to the south of the city. One garden (Cabeça de Veado, 12 km south of the centre of Brasília) had a lawn (700 sq m) of the African grass *Digitaria diversinervis* Stapf. *P. satan* nested in shaded parts of buildings,10 m to 30 m from the lawn, and a colony of *P. ignobilis* was located in a nearby forest 150 m from the lawn, but *P. versicolor* was not seen there. *P. edulis* was cultivated in all the gardens and at the farm. Data were collected on wasps which visited the vines at all the sites. *P. ignobilis* was recorded on the vines in five gardens and *P. satan* and *P. versicolor* in seven of them. All three species were recorded on the vines at the farm.

Social wasps hunt many species of caterpillars. In Brasília the three species of wasps under study were seen to hunt larvae of the heliconiine butterflies *Heliconius melpomene* (Linnaeus, 1758), *H. erato* (Linnaeus, 1758) and *Dione vanillae* (Linnaeus, 1758) (Nymphalidae) which are commonly encountered on *P. edulis*. Caterpillars were not seen on the lawn. *Digitaria diversinervis* is an introduced species and seems to suffer very little from the attacks of native Lepidoptera. The three species of wasps were also observed hunting on other taxa of plants. These included *Citrus* species, *Duranta erecta* Linnaeus, *Pachira aquatica* Aubl, *Solanum* species, parsley, rose and rice.

METHOD AND RESULTS

The activity of a wasp was recorded only when the insect actively searched a leaf. This she did by either flying slowly around the leaf edge or walking on the leaf. However, a wasp which alighted and flew off without showing any sign of searching was not recorded. All the investigations were conducted during sunny weather, with shade temperatures between 18°C and 32°C and in places where wasps were active. Additional observations on the hunting behaviour of other species of social wasps were made at several localities in the region. The investigations on the wasps' behaviour comprised four parts; two on each plant species.

Cutting leaves: the lawn – Methods

From February to April and in October 1987 and February and March 1988 information was collected on *P. satan* and *P. ignobilis* when they visited the lawn at Cabeça de Veado. During the days of investigations the lawn was exposed to strong sunshine almost the entire time. Data on the wasps were collected during six periods, each comprising ten consecutive days. These were two days immediately before mowing, the day of the mowing and the seven days afterwards. On the days of mowing, observations started within 20 min after the mowing had finished. Every day observations were made for two hours per day (09.00 to 11.00 hr). In addition, on three days per ten-day period (the day prior to the mowing, the day of the mowing and the sixth day after mowing) the visits of wasps to the lawn were recorded for six hours continuously (09.00 to 15.00 hr).

Cutting leaves: the lawn – Results

Visits of wasps during ten consecutive days

During six 10-day periods for two hours per day a total of 1,534 visits by the wasps were recorded (1,129 of *P. ignobilis* and 405 of *P. satan*). The number of visits by *P. ignobilis* recorded during a single 10-day period varied 1.36 X (from 166 to 226), while the number of visits by *P. satan* varied 2.14 X (from 42 to 90). The maximum total number of wasps which visited the lawn during a single 20-minute period was 23.

Two analyses were conducted on the data of the wasps' presence during the 10-day periods. Firstly, the numbers of visits on the day of the mowing were compared with the numbers on the nine other days. Secondly, the numbers on the day following the mowing were compared with the numbers on the eight other days when the lawn was not mown. (These were the two days before and the second and subsequent days after the mowing, marked as days -2, -1 and 2 to 7 of figure 1). Both species were encountered more often on the day that the lawn was mown than on any of the nine days when the lawn was not mown. *P. ignobilis* was 4.6 X more abundant than the mean of the other nine days ($X^2 = 187.67$, $P < 0.0001$ at 9 df) and *P. satan* was 8.6 X more abundant ($X^2 = 164.24$, $P < 0.0001$ at 9 df) (Fig. 1). On the day after mowing the numbers of visits of the two species were higher than on other eight days without mowing, but not significantly so ($X^2 = 4.11$ for *P. ignobilis* and $X^2 = 14.97$ for *P. satan* at 8 df).

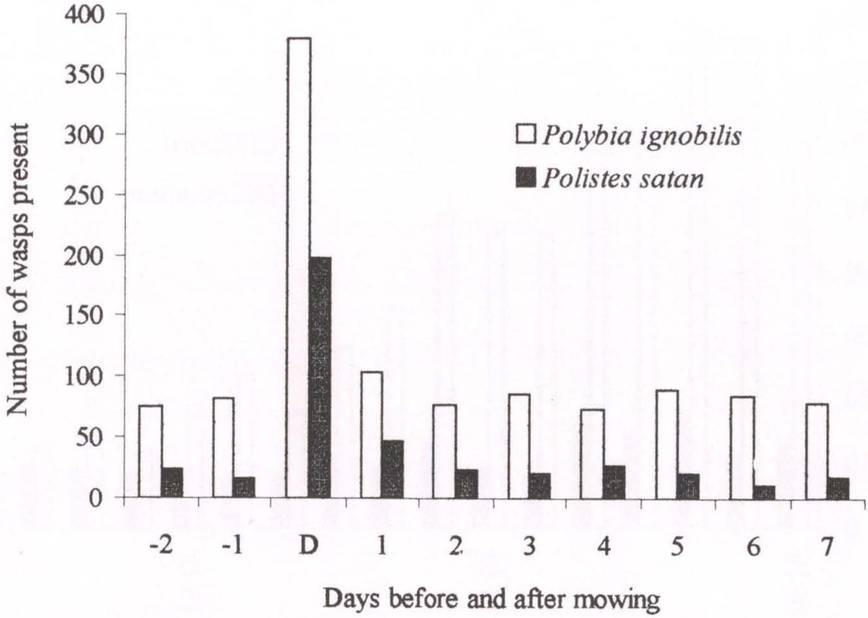

Fig. 1. The numbers of two species of social wasps which hunted on a freshly mown lawn. Wasps were observed for two hours per day during six periods of ten consecutive days each. (D = day of mowing.)

Visits of wasps during six consecutive hours

During the six hours of continuous observations per day over six days a total of 1,181 visits by the wasps were recorded (844 of *P. ignobilis* and 337 of *P. satan*). On each visit most wasps spent a short time on the lawn (estimated at less than three minutes). On the days of mowing the number of visits of *P. ignobilis* totalled 658 and the number recorded on a single day varied 1.5 X (from 87 to 131), while those of *P. satan* totalled 273 and the daily variation was two-fold (from 30 to 59). On the six days when the lawn was not mown a total of 186 visits by *P. ignobilis* were recorded ranging from 24 to 43 per day. Comparative data on *P. satan* were a total of 64 visits and a range of 8 to 14 per day.

On a day of mowing both species were abundant during the period immediately after the grass was cut. *P. ignobilis* reached 40 visits and *P. satan* 23 during the first hour after mowing. During the rest of the day their numbers dropped and after some hours their numbers were similar to those on days when the lawn was not mown (Figs 2, 3). However, the two species differed significantly in their rates of decline during the day ($X^2 = 30.55$, $P = 0.023$ at 17 df). *P. ignobilis* continued to visit the lawn in increased numbers for at least three hours before they showed any substantial reduction (Fig. 2). During the first two hours after mowing the numbers of *P. satan* were higher than for the equivalent period prior to the mowing, but then fell to their previous levels during the third hour (Fig. 3). In contrast the differences in the numbers of wasps of the two species encountered on the lawn during days when the lawn was not mown did not differ significantly ($X^2 = 11.3$; $P = 0.84$ at 17 df).

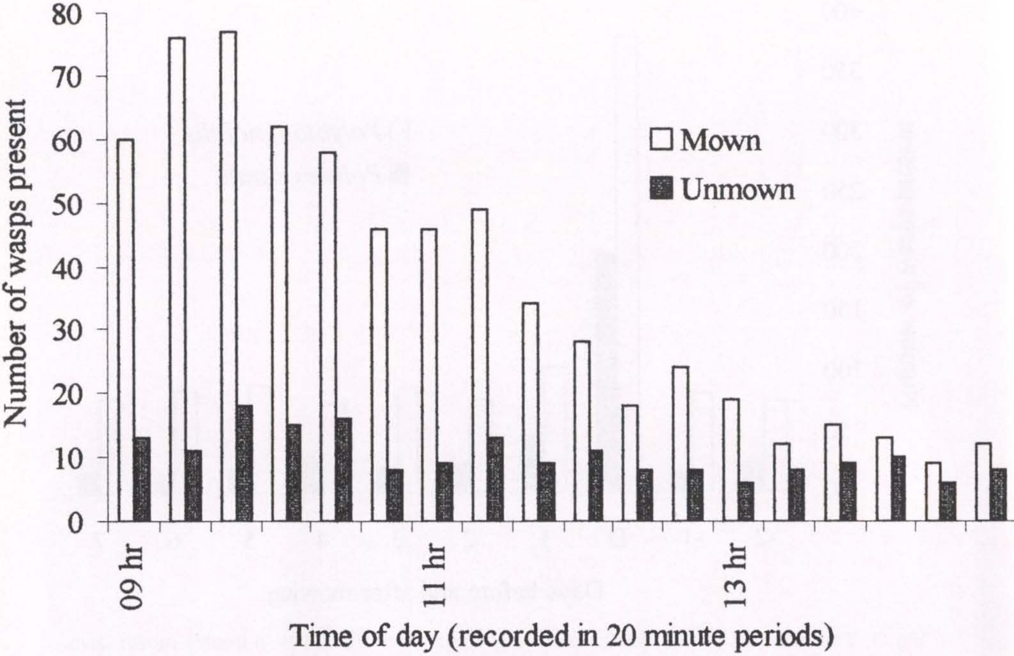

Fig. 2. The numbers of *Polybia ignobilis* which hunted on a lawn when it was unmown and freshly mown. Wasps were observed for six hours per day during six periods of ten consecutive days each.

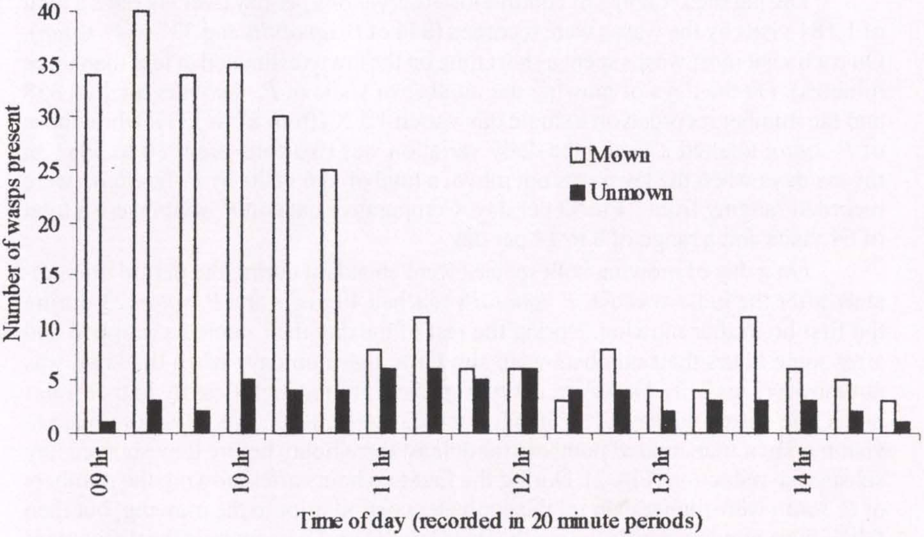

Fig. 3. The numbers of *Polistes satan* which hunted on a lawn when it was unmown and freshly mown. Wasps were observed for six hours per day during six periods of ten consecutive days each.

Cutting leaves: passion vine – Methods

Investigations on *P. edulis* were conducted shortly before or after the tests on the lawn at Cabeça de Veado and also from February to April in 1989 there and in the nine other gardens and on the farm at various times from September to December 1993 and in January to May 1994.

A total of 80 young, fully expanded, undamaged leaves were selected on one part of a vine (being the maximum number which could be conveniently observed by one person) and a small length of white cotton thread was attached to the petiole of each. A margin 1 cm to 1.5 cm long and representing about 5 % of the total leaf area, was cut with scissors from 40 of the leaves and the numbers of cut and uncut leaves which wasps visited were counted. The test was conducted 100 times giving a total of 8,000 leaves offered, each for one hour. At least seven days were allowed between the tests at each site, but sometimes the interval was longer as it depended on the production of new leaves. The exception was at the farm where a field of five hectares provided sufficient plants to conduct more than one test per day and repetitions every day or two.

When each test began it was not known which species of wasp might appear, so the number of leaves considered to have been offered to each species was calculated in the following manner. When at least one individual of a particular species of wasp was seen to visit one of the leaves during a daily test period (of one hour) that species was recorded. Conversely, when a species was not seen on a particular day it was considered to have been absent from the site and the leaves not offered to that species. Employing this criterion, of the 8,000 leaves, 6,000 (sum of first column of data in table I) were offered to the three species on 17, 24 and 34 days.

Cutting leaves: passion vine – Results

The maximum numbers of wasps seen to visit passion vines during a one-hour period were nine *P. ignobilis*, twelve *P. versicolor* and three *P. satan*, but on numerous occasions a particular species was not seen at a locality. As the number of wasps varied so much from place to place and from time to time the data for each species were pooled.

All three species behaved similarly when they visited a freshly cut leaf. Typically a wasp alighted on the upper surface of the leaf, walked immediately to the cut edge, inspected it and often she then passed to the underside of the leaf. The number of visits of *P. versicolor* was significantly greater to the cut versus uncut leaves and, while the number of visits of both *P. satan* and *P. ignobilis* also increased, they were not significantly different (Tab. I).

Applying odour: card and passion vine leaf – Methods

An investigation which entailed applying odour to cards and undamaged leaves was conducted on various dates during 1993 and 1994 in Cabeça de Veado, Sobradinho and four other gardens around Brasília and on the farm. Fresh leaves of passion vine were crushed and immediately the macerate was rubbed lightly onto the upper surface of undamaged leaves of the same plant and onto one side of oblong green cards (4 cm x 5 cm) which were (to humans) of a similar colour and shade to the leaves. For each test 20 leaves and 20 cards with the macerate and 20 leaves and 20 cards without the macerate were used, totalling 80 points of observation. The cards were hung by paper-clips from the branches of the vines. The wasps' visits to the plants and the cards were recorded for one hour per day on 80 days, thus totals of 3,200 leaves and 3,200 cards were each offered for one hour. As with the previous series of tests there were at least seven days between the tests at a site, but the interval depended on the availability of new leaves, while at the farm tests were conducted every day or two.

Table I. The numbers (and percentages) of three species of social wasps which hunted on uncut and freshly cut leaves of passion vines.

Wasp species	Number of leaves offered of each type	Nember of uncut leaves inspected by wasps	Number of freshly cut leaves inspected by wasps	Chi square value	Probability of visiting cut over uncut leaves	Relative increase by cutting leaves
P. versicolor	2720	29 (1.1)	52 (1.9)	6.07	0.014	1.8 X
P. ignobilis	1920	17 (0.9)	31 (1.6)	3.57	0.059	1.8 X
P. satan	1360	9 (0.7)	18 (1.3)	2.39	0.122	2 X

The numbers of leaves and cards considered to have been offered to each species were calculated by the same method as in the previous experiment. When at least one individual of a particular species of wasp was seen to visit a leaf or a card during a test that species was considered as having been tested, whereas a species not seen during a test was considered to have been absent from the site and the leaves and cards not offered to that species. Of the 3,200 of leaves and of cards, a total of 1,440 leaves and the same of cards was considered to have been offered to the three species on 9, 12 and 15 days (sum of first column of data in table II).

Table II. Numbers of visits by three species of social wasps to undamaged leaves of *Passiflora edulis* and to pieces of green card after rubbing them with freshly crushed leaves of the plant.

Wasp species	Number of pairs o leaves and cards offeredf	Numbers of leaves inspected		
		Without odour	Odour added	Probability
Polistes versicolor	600	11	16	Not significant
Polybia ignobilis	480	6	8	Not significant
Polistes satan	360	10	18	Not significant

Applying odour: card and passion vine leaf – Results

All three species were attracted to the leaves painted with macerate more than to the control leaves but none was significantly different either tested separately (Tab. II) or pooled ($X^2 = 0.0603$ at 5 df). As with a cut leaf, typically a wasp alighted on the upper surface of a painted leaf, however the subsequent behaviour was more varied. Sometimes a wasp touched the leaf surface with her antennae and sometimes she walked to the edge of the leaf. Occasionally she passed to the underside of the leaf.

A few individuals visited and inspected cards bearing macerate, but none of them inspected an unpainted card. *P. versicolor* inspected 6 cards with macerate, *P.*

satan visited 11, while *P. ignobilis* visited none. On three occasions individuals of *P. versicolor* alighted on a control card, but flew off immediately without exploring the card.

Additional species: Methods and Results

In order to discover if the behaviour of the three species of wasps which were investigated in the above experiments might be more widespread, some additional notes were collected on other species of wasps and plants around Brasília and around the towns of Goias in Goias State and Patos de Minas in Minas Gerais State. These tests involved cutting the margins of 20 to 50 leaves on plants where wasps were seen to be hunting and observing the wasps' reactions. As in the previous experiment with cut leaves – only young, fully expanded, undamaged leaves were used.

Tests were conducted on eight additional species of social wasps of the genera *Polybia* and *Polistes*. The preliminary results suggest that all of them might be attracted to recently cut leaves (Tab. III), though insufficient data were collected for statistical analysis. During the field work three other species of social wasps were seen to behave similarly. *Parachartergus fraternus* (Gribodo, 1892), *Synoeca surinama* and *Mischocyttarus cerberus styx* Richards, 1940 alighted on leaves and inspected them, presumably in search of prey.

Table III. Records of nine additional species of social wasps which were attracted to freshly cut leaves of thirteen taxa of plants.

Wasp species	Plants	Attraction to cut leaves
Polistes cinerascens de Saussure	*Byrsonima crassa* Niedenzu	12
Polistes erythrocephalus Latreille	*Sabicea brasiliensis* Wernham	3
Polybia fastidiosuscula de Saussure	*Crotalaria* species	7
Polybia liliacea (Fabricius)	*Citrus* species	*
Polybia occidentalis (Olivier)	hot pepper (*Capsicum annuum* Linnaeus)	16
Polybia occidentalis	cocoyam [*Colocasia esculenta* (Linnaeus)]	15
Polybia occidentalis	green cabbage (*Brassica oleracea* Linnaeus)	28
Polybia occidentalis	lettuce (*Lactuca sativa* Linnaeus)	7
Polybia occidentalis	apple mint (*Mentha suaveolens* Ehrh.)	6
Polybia occidentalis	*Styrax ferruginea* Nees & Mart	4
Polybia paulista von Ihering	*Cassia* species	12
Polybia quadricincta de Saussure	green pepper (*Capsicum annuum* Linnaeus)	10
Polybia sericea (Olivier)	rose (*Rosa* sp.)	4
Polybia striata (Fabricius)	*Vernonia* species	9

DISCUSSION

The size of the wasp's hunting problem

A wasp which goes out to hunt is faced with a huge option so she must make some decisions about where to hunt. To my knowledge there is no evidence that social wasps communicate the location of a source of food as social bees do (MICHENER 1974; ROUBIK 1989; O'TOOLE & RAW 1991) and probably each wasp must decide herself where she will hunt (JEANNE *et al.* 1995). A rough, conservative estimate (personal observation, Dra. Ivone Resende Diniz, Dr. Vitor O. Becker, Dr. John D. Hay, personal communication) is of about one million leaves per hectare in the area which included a forest-savanna boundary, which gives a mean of some five thousand leaves per wasp. Furthermore, a wasp might inspect some of the leaves more than once.

Another difficulty which the wasps face is the relative scarcity of prey items in the cerrados. These are the savannas central Brazil; a region with very poor soils and strongly seasonal rainfall. Investigations on various plants have indicated that herbivorous insects occur at very low densities in this biome (LOYOLA & FERNANDES 1993; NASCIMENTO & HAY 1993; PRICE *et al.* 1995). An additional factor which might further complicate the wasps' choice is the very high species diversity of herbivorous insects in the cerrados. The wasps are faced with many species of caterpillars, but all occurring at low densities which might make the formation of a search image of a particular species difficult. The following numbers help to illustrate the situation around Brasília. Some 3,500 species of flowering plants, 1,250 species of butterflies, 8,000 species of moths and 63 species of social wasps have been recorded in the Federal District of Brasília; an area 5,822 km^2 [J.A. Ratter, D.R. Gifford, V.O. Becker (all by personal communication) and Raw http://www.unb.br/zoo/).

Visual cues

Social wasps use sight, scent and taste to locate their prey. However, there seem to be some differences among the species. JEANNE (1972) reported that *Mischocyttarus drewseni* de Saussure, 1857 hunted only by sight, whereas RAVERET-RICHTER & JEANNE (1985) found that scent was more important than sight for *Polybia sericea* and especially so within 50 cm of the prey. These differences might be related to the different habitats used by the two species. *P. sericea* is a species of open savannas, while *M. drewseni* frequents the forest edge (RAW 1992).

A telling comment of HEINRICH (1979) is that "amateur entomologists locate caterpillars by first looking for leaf damage". This method can be very successful in other regions, but it is very rarely successful in the Brazilian cerrados (personal observation, Dra. Ivone Resende Diniz, Dr. Helena Castanheira de Morais, Sr. Kiniti Kitayami, Dr. Vitor O. Becker, Dr. John D. Hay, personal communication). Similarly, as HEINRICH (1993) surmised, for avian predators the visual evidence of leaf damage seems to be less used in tropical than in temperate environments.

In many parts of the tropics the disadvantage of using visual evidence of leaf damage to detect the presence of caterpillars is that, for temporary structures, leaves can reach a considerable age. In the strongly seasonal climate of the Brazilian cerrados the longevity of leaves of many species appears to be about ten months (NASCIMENTO & HAY 1993; MORAIS *et al.* 1995, and personal observation) while, among the Panamanian tree species investigated by COLEY (1988), the leaf life-time was up to 35 months. A leaf might be damaged during the first weeks of its life and bear the evidence for many months afterwards. There is some doubt about the relevance of leaf age for caterpillars. Some studies have demonstrated that the expansion of the leaf affects the growth and survivorship of caterpillars (AIDE & LONDONO 1989) and preliminary data from the cerrados suggest that leaves suffer most herbivore damage during the first few weeks of their existence (RAW & HAY 1985; MARQUIS *et al.* 1993; NASCIMENTO & HAY 1993). However, in some tropical environments leaf age is said to be unimportant to feeding caterpillars (JANZEN & WATERMAN 1984; JANZEN 1993). Anyhow, in the present investigation the wasps did not appear to distinguish between younger and older leaves.

Numbers of wasps

The total numbers of wasps which were recorded visiting leaves during this investigation may be considered small (2.3 visits per 100 leaf-hours of observation). Nonetheless, this number is artificially inflated because experiments were conducted only when and where wasps were seen to be hunting in some numbers. However, the low numbers are due to at least two factors. Firstly, only three species of predators were investigated. Data were not collected on predatory insects of other taxa, nor on the birds and lizards which are important insectivores in the region and were often seen in the study areas. The second factor is the large search area of the wasps which contained a huge number of leaves.

Leaf odours as cues

It is reasonable to presume that, when leaving the nest on a hunting trip, a social wasp does not fly to any plant at random and that she may use cues in her search for prey. However, the decision about which of the many plants and the huge number of available leaves a wasp might inspect could be based on any of several indicators. The present investigation demonstrates that the three species of wasps were attracted to the odours of freshly cut leaves when hunting. This evidence suggests that the wasps used these odours as indirect olfactory cues to indicate whether they might be in the vicinity of a potential prey. Presumably, as previous authors have reported (EVANS & WEST-EBERHARD 1973; JEANNE 1972; RAVERET-RICHTER & JEANNE 1985) the wasp then employs direct cues (visual, olfactory or both) to locate a prey item. (The question of leaf odour was eliminated from the last mentioned study as the prey items offered were larvae of another social wasp, *Polistes canadensis* Linnaeus, 1758).

Polybia ignobilis and *Polistes satan* were attracted in substantial numbers to the lawn when it was freshly mown and especially during a short period immediately after the grass was cut. At a more detailed scale the significantly larger numbers of *P. ignobilis* and *Polistes versicolor* which were more attracted to freshly cut leaves of passion vines than to uncut leaves demonstrates the importance of the recently damaged leaf. The attraction of a few wasps to cards whose surface had been rubbed with a freshly crushed leaf suggests that the odour of the leaf rather than the visual damage it suffered is important to the hunting wasp; a point which warrants further investigation. One question (raised by Dr. Peter W. Price, personal communication) is whether the wasps were foraging for moisture on the damaged leaves. It is doubtful that they did so during the investigation. Brasília's mean annual rainfall is 1,500 mm; most of it during the seven months wet season when the study was conducted and during that period water is plentiful.

When a wasp alighted on a leaf of *Passiflora edulis* apparently she recognized the edge visually and inspected only or principally that part of the leaf as anthocorid bugs do (EVANS 1976). As might be expected with the differences in their powers of perception, the wasps did not appear to distinguish visually between entire leaves and damaged ones as birds are able to do (HEINRICH & COLLINS 1983; HEINRICH 1993). Anyhow, it would seem unnecessary for a social wasp to resort to a relatively sophisticated analysis of a comparison of leaf shape or age when they are able to use a search strategy based on the olfactory evidence of extremely recent damage which might indicate the continuing presence of the culprit.

So far as I know, this is the first study on this aspect of the hunting of social wasps and the first which demonstrates the use of indirect chemical cues by any predators in the field. The final part of the study was conducted on other central Brazilian species and suggests that the attraction to freshly damaged leaves might be a common phenomenon among social wasps. (This hunting strategy might be still more widespread among social wasps for I have seen *Vespula vulgaris* (Linnaeus) attracted in numbers to freshly mown lawns in England)

The above comments might seem to be in conflict with Raveret-Richter's record (cited in MONTILLOR & BERNAYS 1993) that wasps recognized leaves rolled by caterpillars. A rolled leaf is visually very characteristic of a particular category of prey and this peculiarity must aid the wasp's memory. Furthermore, the leaf remains rolled for a short period; it either unrolls or is shed. Therefore, a wasp wastes little time searching old leaves which no longer contain caterpillars. Around Brasília both *P. satan* and *P. erythrocephalus* Latreille, 1813 take moth and skipper caterpillars from rolled leaves and the wasps' systematic searches indicate that some wasps learn to recognize a rolled leaf and at some sites individual wasps restrict their hunting largely to this type of prey (personal observation).

Not surprisingly, caterpillars employ some strategies to avoid predation. The predator-avoiding strategies of caterpillars have been summarized by HEINRICH (1979) and, although his analysis focused on avian predation in a temperate-region, most of the components he identified apply equally to tropical species which insects prey on. Two components are pertinent here. Generally, after a feeding bout a caterpillar moves from an unfinished leaf to a distant one before feeding again and, secondly, in several species the caterpillar snips off a partially-eaten leaf after feeding on it. Presumably both activities reduce the probability of attack on the caterpillar by a predator which would notice the damage; one by distancing the animal from the site of the evidence and the other by removing the evidence.

HEINRICH (1979) noted that the caterpillars which remained exposed during the day were non-palatable species, but at least in some instances, this strategy does not seem to function well against social wasps. The three species of caterpillars which the wasps hunted during this investigation eat leaves of *P. edulis* and they possess toxic compounds derived from their food (BROWN *et al.* 1991). Furthermore, in Brasília I have seen *P. satan* take several of the aposematic caterpillars of *Danaus plexippus* (Linnaeus, 1758) (Nymphalidae) from *Asclepias curassavica* Linnaeus (Asclepiadaceae) plants. These caterpillars are also well known for being unpalatable to birds (BROWER 1969).

Use of spatial memory

The use of olfactory cues cannot be the only factor used in selecting a potentially rewarding hunting area because the wasps are not always attracted to freshly cut leaves. Therefore, another factor which influences the numbers of wasps which visit a site is that the wasps memorize the specific plants and sites where they hunted previously and return to them. A wasp's ability to learn a site of previous successful hunting was used by RAVERET-RICHTER (1990) who trained *Polybia sericea* to return to an experimental site where the wasps had located prey. In the present study this ability was demonstrated by the large numbers of visits to the lawn on the day after it was mown even though, presumably, the hunting had not been rewarding there. It is believed that the leaves emitted an odour only for an hour or two after the mowing because the numbers of visits fell to pre-mowing levels during the day so it is doubtful that an odour remained on the following day. The use of a short-term memory of previous successful hunting by social wasps has been demonstrated (RAVERET-RICHTER 1990; MONTILLOR & BERNAYS 1993) and its role in predation by insects has been discussed by OLLASON (1980).

The third trophic level

The three species of social wasps under study were attracted to the odours of artificially, freshly cut leaves. Another generalist predator, the anthocorid bug, *Orius insidius* behaved likewise (REID & LAMPMAN 1989). In contrast, predatory mites and parasitoid wasps are strongly attracted to leaves only when they are damaged by a herbivore and release volatile terpenoids, but not when the leaf is damaged artificially (SABELIS & VAN DE BAAN 1983; DICKE *et al.* 1990, TURLINGS *et al.* 1990). For example, a predatory mite, *Tetranychus urticae* was attracted to the odour of an undamaged or a mechanically damaged leaf, but strongly preferred the odour of a leaf damaged by a herbivorous mite to either (TAKABAYASHI & DICKE 1997). It is possible that a specialist predator might prefer the particular odour a leaf emits as a result of damage caused by its herbivorous prey, whereas a generalist might be attracted to the odour following any mechanical damage. It would seem unnecessary for a generalist to distinguish between the various odours resulting from attacks by different herbivores when the predator would regard all of them as potential prey. It has been suggested that these plant volatiles might have evolved to attract specific arthropod predators to the presence of their particular herbivorous prey (WHITMAN 1988; DICKE *et al.* 1990, TURLINGS *et al.* 1991). These volatile substances have been called synomones, which are chemical signals that benefit both the sender and recipient (DICKE & SABELIS 1988; WHITMAN 1988).

Demonstration in the present work of the use of general plant odours by generalist arthropod predators leads one to surmise that the role of these predators at the third trophic level of plant defence might prove to be as widespread a phenomenon as the odours emanating from damaged leaves and as the predators capable of perceiving them. The adverse effect of herbivores on the growth of tropical and temperate plants and the role of the predators have been clearly demonstrated (MARQUIS 1984; COLEY 1988; MARQUIS & WHELAN 1994).

Much of the work on the carnivore's perception of herbivore-induced plant volatiles has investigated the role of parasitoids. However, FAETH (1994) noted that parasitoids do not kill the herbivore until after it has finished feeding so any effect they might have on plant fitness could only be manifest in the next generation of the herbivore. This argument does not obtain with predators which remove their prey immediately, therefore, any change in plant fitness which results in the production of these odours may be more easily investigated with these animals.

Frequency of visits

An additional piece of information which was derived from the above investigations is the frequency at which the wasps searched leaves. During the experiments on passion vines a total of 225 (156 + 69) visits by the three species was recorded and the total number of leaves offered was 9,600 (6,400 + 3,200). Each leaf was observed for one hour so a wasp averaged one visit per 42. 7 leaves per hour. When one considers that sites where the wasps were numerous and plants which they visited there were selected for observation, the frequency is considered to be low.

Final comment

Apparently the three species of social wasps employ two factors in the selection of a place to search for prey and these obviate the need for recruitment of nest-mates.

Each wasp remembers the place to which she was strongly attracted and returns to hunt there. However, a strong attraction is not necessarily related to a reward and the wasps returned in numbers to a place where they hunted without encountering increased numbers of prey.

The wasps utilize the scent of freshly damaged leaves to select the area where they hunt and also the particular leaves which they inspect.

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