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Research article

Nesting site selection by wasps in the Guianese rain forest

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Summary

In the edge of the rain forests in French Guiana, the large leaves of young *Astrocaryum sciophilum*, a palm tree with long thin spines (up to 9 cm) along their central vein, shelter significantly more mason as well as social wasps' nests, than leaves of other plants. Other such plants include older conspecific individuals with spines, but compound leaves, and young *Bactris simplifrons*, a palm tree with similar leaves but devoid of spines. The choice of these leaves is due to the association of two factors: (1) these large leaves with a concave underside offer good protection against inclement weather, and (2) the spines on which the wasps' nests are anchored serve as "acquired pedicels", offering protection against ant predation. As a consequence, the wasps' nests are found under these leaves in both inter- and intraspecific clusters.

Introduction

In the tropics, social wasp nest architecture and nest site selection have evolved under the influence of at least two kinds of selection pressure: weather, and a strong predation rate from ants and vertebrates. For protection from inclement weather, nests are frequently built under shelters such as the entrances of caves, overhanging rocks, human constructions and under the large leaves of certain plants. Nevertheless, some Epiponini build large nests protected by an envelope, directly exposed to inclement weather.

Due at least in part to predation pressure from ants, nests of Polistinae primitively had a pedicel that workers rubbed with their gaster to add substances repellent to ants and later evolved a means of protection using an envelope (Jeanne,

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1970a, 1975a; Turillazzi and Ugolini, 1979; Kojima, 1983; Henderson and Jeanne, 1989; Keeping, 1990; Carpenter, 1991; Wenzel, 1993). Nests of certain Polistinae and Vespinae have both envelope and pedicel, or have a pedicel during the founding period and then have an envelope (Wenzel, 1991).

Predation on wasp colonies by vertebrates can also be intense (Jeanne, 1970b; 1975a; 1991; Windsor, 1976; Yamane, 1996). Nests of many species of social wasps are cryptic and well camouflaged in a natural background, involving such factors as shape, coloration and transparency. Nest site selection is an important part of such crypsis, and in some species there is intraspecific variation in the details of construction correlated with whether a nest is built on a small or a large leaf (Jeanne, 1991; Jeanne and Morgan, 1992; Wenzel and Carpenter, 1994). Also, intra- and interspecific nesting associations of wasps have been recorded by several authors (Janzen, 1969; Jeanne, 1975b, 1978; Windsor, 1972; Herre et al., 1986; Joyce, 1993; London and Jeanne, 1996).

Shelters offered by large leaves can be more or less favorable as wasp nesting sites, depending on different factors related to the plant species. We observed by chance that the large, rigid leaves of a young palm tree with a concave underside and long spines distributed under the principal vein sheltered several wasps' nests directly attached to the spines. As a consequence, we hypothesized that this particular situation (long spines under large leaves) is very attractive to wasps as a nesting site.

Materials and methods

This work was undertaken near Sinnamary, French Guiana, over the course of three years (December 1992; July 1994 and February 1995) on the *Citrus grandis* trees situated along the 900 m long edges of a plantation, and a part of the forest edge (section 800 m long, 5 m wide) around this plantation plus 500 m along a small stream at Petit Saut.

We recorded the relationships between the nests of social wasps and plant species, including the effect of the size of the leaves: small leaves (less than 12 cm in length); medium-sized leaves (15 cm to 20 cm in length; 8 to 15 cm in width); and large leaves (more than 20 cm in length and 15 cm in width). A detailed analysis was then undertaken comparing the percentages of wasp nidification on *Citrus* trees (small leaves); *Clusia* sp. (medium-sized leaves); and four plant species with large leaves. We counted the number of wasps' nest per plant and the number of leaves per plant for large-leaved species, while for *Citrus* and *Clusia* we made an evaluation of the number of leaves per tree.

For palm trees (Arecaceae), we compared the juveniles (less than 1 m in height) of two species (characterized by leaf dimorphism as are numerous other palm tree species, with juveniles having simple leaves while older trees have compound leaves) whose simple leaves differ by the presence of long spines along the underside of the central vein in *Astrocaryum sciophilum* (common palm tree known as "mourou-mourou"), while *Bactris simplifrons* have none (comparison: presence versus absence of spines). For *A. sciophilum*, we compared the simple leaves of juvenile trees with the compound leaves of older trees of a height comprised between 2 m and 4 m (presence of spines of 3 to 9 cm long in both cases; comparison: difference in leaf shape).

For statistical comparisons, we used StatXact software and the two-tailed Fisher exact test for comparisons of distributions (Ludwig and Reynolds, 1988).

Results and discussion

Diversity of plants chosen as shelter

The density of wasps' nests was only slightly inferior on the plantation (16 wasps' nests for 900 m of plantation edge; 75 trees) than in the forest edge (17 wasps' nest for 800 m) where we recorded 760 shrubs and young trees of a size comprised between 1.5 and 9 m. It seems therefore that the well-exposed plantation does not hinder wasp nest construction in comparison to the shrubby, more shaded forest edge.

We recorded social wasps' nests on 25 plant species (Table 1), mason wasps being present only under leaves of *A. sciophilum.* Of the 11 polistine wasp species recorded (those of Table 2 plus *Angiopolybia pallens* nesting on *Cordia nodosa*, a myrmecophytic Boraginaceae situated along the forest edge) large nests of *Polybia quadricincta*, attached to a small horizontal branch, were only recorded on the plantation on *Citrus* trees occupied by *Azteca chartifex* or *Dolichoderus bidens*, two dolichoderine ant species with very populous colonies. These large nests (as well as those of *Angiopolybia pallens*), easy to see (and exposed to vertebrate predation pressure if any) are probably protected against army ant predation by the arboreal ants with which they share the trees. Army ants (Ecitoninae) are among the principal predators of wasps in the Neotropics (Jeanne, 1975; Chadab, 1979; Hölldobler and Wilson, 1990; Yamane, 1996) whereas wasp protection by arboreal ants has been previously recorded (Espelie and Hermann, 1988; Jeanne, 1991; Joyce, 1993).

Determination of criteria influencing the choice of the nesting site

Juvenile *A. sciophilum* plants sheltered more social and mason wasps' nests than older *A. sciophilum* plants and other species, including *B. simplifrons* (Fig. 1). Young *B. simplifrons* have leaves of the same size and shape as *A. sciophilum*, but are devoid of spines; and old *A. sciophilum* (and numerous other palm tree species) have spines but compound leaves. Therefore, it is the combination of two factors, large leaves and the presence of spines along the central vein, which renders *A. sciophilum* a very good shelter for wasps' nests (Fig. 2). As a consequence, the nests of several wasp species can be concentrated on the rare young *A. sciophilum*, even under the same leaf, both intra- and interspecifically in mutual tolerance. Thus, we recorded 37 mason wasps' nests, one eumenid's nest, plus 25 eusocial wasps' nests (total = 63) for 20 young *A. sciophilum.*

The long thin spines (up to 9 cm) play the role of pedicel and protect wasps' nests against ant attacks: we observed *Polistes* spp. rubbing both the pedicel and the spine

Table 1. Different plants sheltering wasps' nests recorded during field studies (*: one large amphora-shaped nest of *Angiopolybia pallens* Lepeletier; **: large nests of *Polybia quadricincta* Saussure, attached to branches while all others sheltered under leaves; numbers in superscript indicate the corresponding number of wasps' nests; see Table 2 for the identification of other wasp species). In this series, only young *A. sciophilum* individuals sheltered several mason wasps' nests (37 nests for 13 trees) and several social wasps' nests (26 nests for 15 trees)

Plant species	Plant family	No. plants recorded	
		with wasps' nest	Total
Plants with large leaves			
Astrocaryum sciophilum (young)	Arecaceae	15	20
Bactris simplifrons (young)	Arecaceae	1	18
Heliconia sp.	Musaceae	5	49
Renealmia sp.	Zingiberaceae	2	30
Undetermined	Maranthaceae	25	350
Undetermined	Melastomataceae	2	12
Plants with medium-sized leaves			
Cecropia sciadophylla	Cecropiaceae	3	> 1000
Clusia sp. (river side)	Clusiaceae	7	67
Plants with small leaves			
Aechmea mertensii (epiphyte)	Bromeliaceae	4	120
Bellutia grossularioides	Melastomataceae	3	> 1000
Citrus grandis (plantation)	Rutaceae	[5]**16	75
Cordia nodosa	Boraginaceae	*1	?
Croton matourensis	Euphorbiaceae	2	> 1000
Gupia glabra	Celastraceae	2	?
Icertia coccinea	Rubiaceae	5	> 1000
Mahurea palustris (river side)	Clusiaceae	3	52
Mangifera indica	Anacardiaceae	2	5
Passiflora coccinea	Passifloraceae	1	> 1000
Platonia edulis	Rubiaceae	1	?
Rhinorea sp.	Violaceae	1	?
Solanum lanciferum	Solanaceae	1	> 1000
Tococa sp.	Melastomataceae	2	150
Vismia guyanensis	Hypericaceae	1	> 1000
Vismia latifolia	Hypericaceae	[1]*2	> 1000
Vismia sessilifolia	Hypericaceae	2	> 1000
Total		110	

to which it is attached (Fig. 2). Species such as *Polybia affinis* and *P. bistriata* that lack a petiole in their nest architecture attach their nests directly to one or more often to several spines and so have pedicels furnished by the supporting plant (Fig. 2).

Among the other plant species compared, we did not record significant differences in the percentages sheltering social wasps' nests on the scale of entire plants (Fig. 1). A comparison which took the number of leaves into account (Table 2) permitted us to confirm that *A. sciophilum* clearly sheltered significantly

Table 2. Diversity of wasp species associated with six plant species, and influence of the size of the leaves on nesting site selection by these wasps (*: incipient colonies; their number is presented in superscript; **: attached to branches while all others sheltered under leaves). Comparisons of the ratios between the number of social wasps' nests and the number of leaves of the different plant species

A. sciophilum vs. *B. simplifrons*	$p < 0.001$	*B. simplifrons* vs. *Citrus grandis*	$p < 0.001$
A. sciophilum vs. *Heliconia* sp.	$p < 0.001$	*Heliconia* sp. vs. *Renealmia* sp.	$p = 0.25$
A. sciophilum vs. *Renealmia* sp.	$p < 0.001$	*Heliconia* sp. vs. *Clusia* sp.	$p < 0.05$
A. sciophilum vs. *Clusia* sp.	$p < 0.001$	*Heliconia* sp. vs. *Citrus grandis*	$p < 0.001$
A. sciophilum vs. *Citrus grandis*	$p < 0.001$	*Renealmia* sp. vs. *Clusia* sp.	$p = 0.94$
B. simplifrons vs. *Heliconia* sp.	$p = 0.44$	*Renealmia* sp. vs. *Citrus grandis*	$p < 0.001$
B. simplifrons vs. *Renealmia* sp.	$p = 0.051$	*Clusia* sp. vs. *Citrus grandis*	$p < 0.001$
B. simplifrons vs. *Clusia* sp.	$p < 0.001$		

	A. sciophil.	*B. simplif.*	*Helicon.* sp.	*Renealm.* sp.	*Clusia* sp.	*Citrus grandis*
Unidentified mason wasps	37					
Zethus binodis (F.) (Eumeninae)	^{1}*1					
Polistinae						
Agelaia cajennensis (F.)						1
Mischocyttarus prominulus Richards	^{2}*2					
Polistes geminatus geminatus Fox	^{1}*1		^{1}*1	1		^{1}*1
Polistes pacificus (F.)	^{2}*3				1	^{1}*2
Polybia affinis Buysson	12	1	1	1	3	1
Polybia bistriata (F.)	2		2		1	5
Polybia micans Ducke	1					**5
Polybia scrobalis surinama Richards	3	1	1		2	
Pseudopolybia langi Bequaert	^{1}*1					
Total/polistine wasps' nests	26	2	5	2	7	16
No. of plants	20	18	49	30	67	75
No. leaves total	98	78	532	711	> 3350	> 75000
No. wasps' nests per 100 leaves	6.53	2.74	0.94	0.28	0.21	0.02
Size of the leaves	large	large	large	large	medium	small

more social wasps' nests than all other plant species compared. The differences between other plant species having large leaves were not significant, while there were significant differences between *Clusia* sp. (medium-sized leaves) and both *B. simplifrons* and *Heliconia* sp., but not between *Clusia* sp. and *Renealmia* sp. (large leaves); and the difference between *Citrus grandis* (small leaves) and all the other plant species compared was always significant. It appears therefore that for wasps that build their nests under shelter two factors influence social wasp nest placement: the size of the leaves and the presence of long spines under the leaves.

The concentration of nests associated with *A. sciophilum* also permitted a concentration of parasitic mantispids. We therefore observed a total of 14 individuals preparing to enter two nests of *Polybia scrobalis surinama*. As previously described (Dejean and Canard, 1990) males and females met around the nests, and after mating, the females entered the nests.

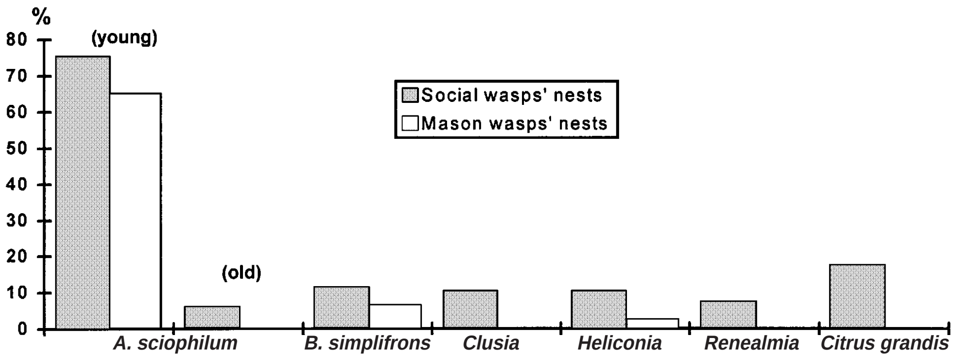

Figure 1. Comparisons of capacity of different plant species for sheltering social and mason wasps' nests.

Percentage of trees sheltering social wasps' nests (statistical comparisons: Fisher exact test). For number of plants and wasps' nests, see Table 2.

A. sciophilum: young vs. old	$p < 0.001$	*B. simplifrons* vs. *Renealmia* sp.	$p = 0.62$
A. sciophilum vs. *B. simplifrons*	$p < 0.001$	*B. simplifrons* vs. *Citrus grandis*	$p = 0.26$
A. sciophilum vs. *Clusia* sp.	$p < 0.001$	*Clusia* sp. vs. *Heliconia* sp.	$p = 0.79$
A. sciophilum vs. *Heliconia* sp.	$p < 0.001$	*Clusia* sp. vs. *Renealmia* sp.	$p = 0.43$
A. sciophilum vs. *Renealmia* sp.	$p < 0.001$	*Clusia* sp. vs. *Citrus grandis*	$p = 0.13$
A. sciophilum vs. *Citrus grandis*	$p < 0.001$	*Heliconia* sp. vs. *Renealmia* sp.	$p = 0.70$
B. simplifrons vs. *Clusia* sp.	$p = 0.92$	*Heliconia* sp. vs. *Citrus grandis*	$p = 0.17$
B. simplifrons vs. *Heliconia* sp.	$p = 0.98$	*Renealmia* sp. vs. *Citrus grandis*	$p = 0.47$

Percentage of trees sheltering mason wasps' nests

A. sciophilum vs. *B. simplifrons* $p < 0.001$

This study demonstrates that the large leaves of several plants in the forest edge favor wasp nest installation, providing good protection against inclement weather (and probably vertebrate predation, mostly by birds, because the nests are hidden as the leaves are close to the ground and the underside is concave). Among them a peculiar phenomenon concerns young *A. sciophilum* which are particularly chosen due to the presence of spines along the principal vein of the leaves. As a consequence, several wasps' nests can be concentrated under the same young *A. sciophilum.* This concentration, which is possible thanks to intra- and interspecific tolerance (intraspecific groups of nests being known in several wasp species; Jeanne, 1978; Itô, 1993), supports the inference that the determination of the choice of this kind of nesting site by founding individuals and/or the survival of the nests is not likely due to chance. The selection of young *A. sciophilum* may be opportunistic for wasp species building nests with a pedicel and a single comb (good protection against inclement weather plus the presence of spines; nests are sometimes built at the extremity of a small twig). For species that build the envelope from the beginning of nest construction, the selection of young *A. sciophilum* corresponds to a remarkable behavioral flexibility. In this case, the wasps do not use the principal vein of the leaves as they do with other plant species, but the spines that serve as an "acquired pedicel".

At least for *Polybia affinis*, the species most frequently recorded, we propose the following scenario: although they have the choice between numerous possibilities,

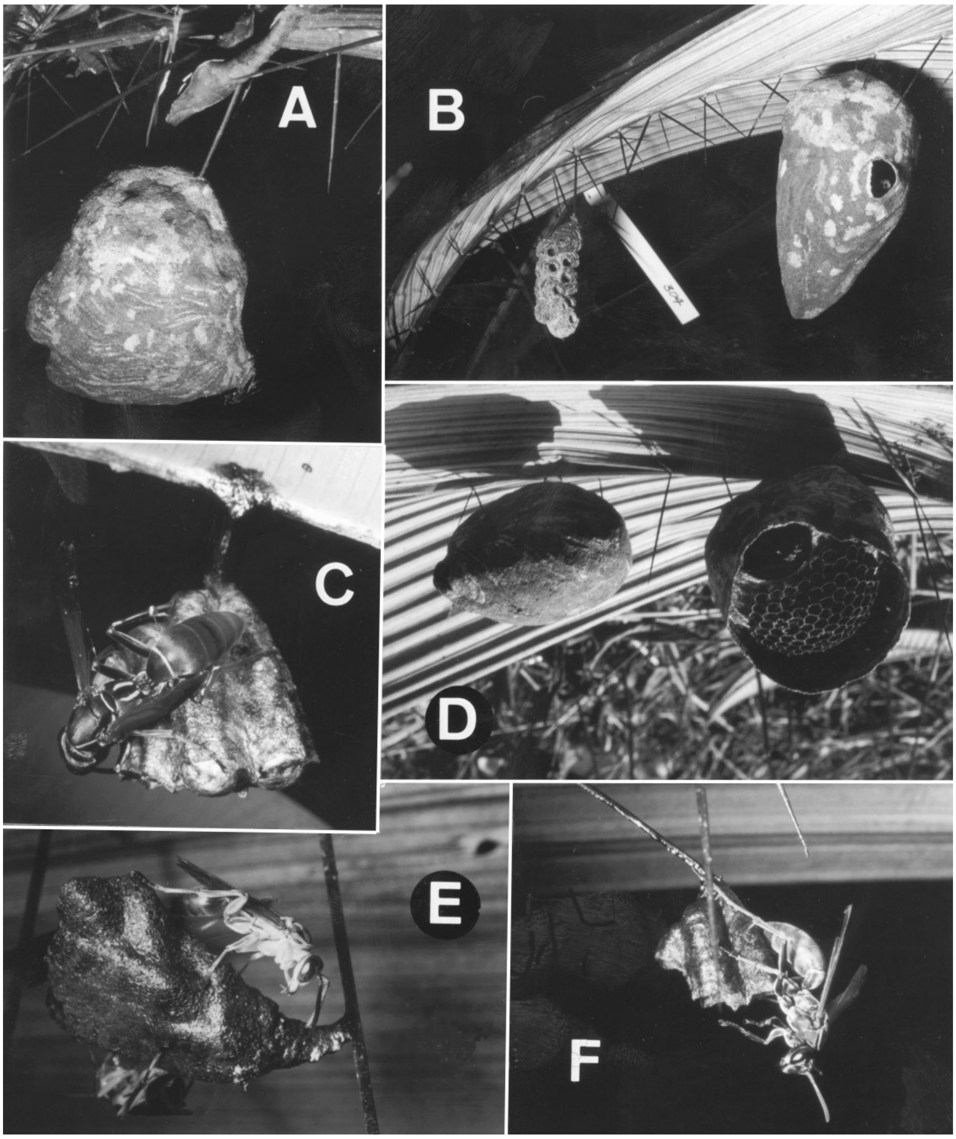

Figure 2. Different mason and social wasps' nests attached to a spine of *A. sciophilum*. (A) Nest of *Polybia affinis* hanging from one single spine. (B) Nest of a mason wasp and a nest of *P. affinis* under the same leaf. (C) Foundation of *Polistes pacificus*, the pedicel is attached to the principal vein of a large leaf of *Heliconia* sp. (D) Nests of *Polybia affinis* in several positions. (E) Nest of *Mischocyttarus prominulus* attached to a spine. (F) Foundation of *Polistes pacificus*, note the brightness of the thorn and the pedicel of the nest, probably due to the addition of oral secretions, in comparison with the thorn situated in the foreground

they nest under the leaves of *A. sciophilum* in what might be considered a kind of learned behaviour, as seen in various species of the genus *Polistes* (Wenzel, 1996). This "tradition" is transmitted by individuals who survived thanks to prior installation under the leaves of young *A. sciophilum* and who search, as a result, for the same kind of nesting site for their new installation.

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References

Carpenter, J.M., 1991. Phylogenetic relationships and the origin of social behavior in the Vespidae. In: *The Social Biology of Wasps* (K.G. Ross and R.W. Matthews, Eds.), Cornell University Press, Ithaca. pp. 7–32.

Chadab, R., 1979. Army-ant Predation on Social Wasps. Ph. D. dissertation, University of Connecticut, Storrs.

Dejean, A. and M. Canard, 1990. Reproductive behaviour of *Trichoscelia santareni* Navas (Neuroptera, Mantispidae) and parasitization of the colonies of *Polybia diguetana* R. du Buysson (Hymenoptera, Vespidae). *Neuroptera Internat. 6*:19–26.

Espelie, K.E. and H.R. Hermann, 1988. Congruent cuticular hydrocarbons: biochemical convergence of a social wasp, an ant and a host plant. *Biochem. Syst. Ecol. 5*:505–508.

Henderson, G. and R.L. Jeanne, 1989. Response of aphid tending ants to a repellent produced by wasps (Hymenoptera: Formicidae, Vespidae). *Ann. Entomol. Soc. Am. 82*:516–519.

Herre, E.A., D.M. Windsor and R.B. Foster, 1986. Nesting associations of wasps and ants on lowland Peruvian ant-plants. *Psyche 93*:321–330.

Hölldobler, B. and E.O. Wilson, 1990. *The Ants.* The Belknap Press of Harvard University Press. Cambridge. 732 pp.

Itô, Y., 1993. *Behaviour and social evolution of wasps. The communal aggregation hypothesis.* Oxford University Press, Oxford. 159 pp.

Janzen, D.H., 1969. Birds and the ant x acacia interaction in central America, with notes on birds and other myrmecophytes. *Condor 71*:240–256.

Jeanne, R.L., 1970a. Chemical defense of brood by a social wasp. *Science 168*:1465–1466.

Jeanne, R.L., 1970b. Note on a bat (*Phylloderma stenops*) preying upon the brood of a social wasp. *J. Mammalogy 51*:624–625.

Jeanne, R.L., 1975a. The adaptativeness of social wasp nest architecture. *Quart. Rev. Biol. 50*: 267–287.

Jeanne, R.L., 1975b. Nest site selection by *Metapolybia* in Costa Rica (Hymenoptera, Vespidae). *J. Kansas Entomol. Soc. 48*:285–290.

Jeanne, R.L., 1978. Intraspecific nesting associations in the Neotropical social wasp *Polybia rejecta* (Hymenoptera: Vespidae). *Biotropica 10*:234–235.

Jeanne, R.L., 1991. The swarm-founding Polistinae. In: *The Social Biology of Wasps* (K.G. Ross and R.W. Matthews, Eds.), Cornell University Press, Ithaca. pp. 191–231.

Jeanne, R.L. and R.C. Morgan, 1991. The influence of temperature on nest site choice and reproductive strategy in a temperate zone *Polistes* wasp. *Ecol. Entomol. 17*:2:135–141.

Joyce, F., 1993. Nesting success of rufous-naped wrens (*Campylorhynchus rufinucha*) is greater near wasp nests. *Behav. Ecol. Sociobiol. 32*:71–77.

Keeping, M.G., 1990. Rubbing behavior and morphology of Van der Vecht's gland in *Belonogaster petiolata* (Hymenoptera: Vespidae). *J. Insect Behav. 3*:85–104.

Kojima, J., 1983. Defense of the pre-emergence colony against ants by means of a chemical barrier in *Ropalidia fasciata* (Hymenoptera, Vespidae). *Japan. J. Ecol. 33*:213–223.
London, K.B. and R.L. Jeanne, 1996. Alarm in a wasp-wasp nesting association: do members signal cross-specifically? *Insectes soc. 43*:211–215.
Ludwig, J.A. and J.F. Reynolds, 1988. *Statistical ecology.* John Wiley & Sons, New York.
Turillazzi, S., 1991. The Stenogastrinae. In: *The Social Biology of Wasps* (K.G. Ross and R.W. Matthews, Eds.), Cornell University Press, Ithaca. pp. 75–98.
Turillazzi, S. and A. Ugolini, 1979. Rubbing behaviour in some European *Polistes* (Hymenoptera Vespidae). *Monit. Zool, Ital. (N.S.) 13:*129–142.
Wenzel, J.W., 1991. Evolution in nest architecture. In: *The Social Biology of Wasps* (K.G. Ross and R.W. Matthews, Eds.), Cornell University Press, Ithaca. pp. 480–519.
Wenzel, J.W. 1993. Application of the biogenetic law to behavioral ontogeny: A test using nest architecture in paper wasps. *J. Evol. Biol. 6*:229–247.
Wenzel, J.W., 1996. Learning, behaviour programs, and higher-level rules in nest construction of *Polistes*. In: *Natural History and Evolution of Paper-Wasps* (S. Turillazzi and M.J. West-Eberhard, Eds.), Oxford University Press, Oxford. pp. 58–74.
Wenzel, J.W. and J.M. Carpenter, 1994. Comparing methods: Adaptive traits and tests of adaptation. In: *Phylogenetic and Ecology* (P. Eggleton and R.I. Vane-Wright, Eds.), Academic Press, London. pp. 79–101.
Windsor, D.M., 1972. Nesting association between two Neotropical Polybiine wasps (Hymenoptera, Vespidae). *Biotropica 4*:1–3.
Windsor, D.M., 1976. Birds as predators on the brood of *Polybia* wasps (Hymenoptera: Vespidae: Polistinae) in a Costa Rican deciduous forest. *Biotropica 8*:111–116.
Yamane, S. 1996. Ecological factors influencing the colony cycle of *Polistes* wasps. In: *Natural History and Evolution of Paper-Wasps* (S. Turillazzi and M.J. West-Eberhard, Eds.), Oxford University Press, Oxford. pp. 75–97.

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