

Variation in Reproductive Strategy of the Tropical Paper Wasp, *Ropalidia fasciata* (Hymenoptera: Vespidae), in Okinawa in Relation to Island Environmental Conditions¹

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ABSTRACT: The tropical paper wasp, *Ropalidia (Icariola) fasciata* (F.), nests on leaves of gramineous plants (*Miscanthus sinensis* Andus. and sugarcane) in Okinawa, where there are frequent, strong typhoons. In Taiwan and Java, where the effects of typhoons are less severe, most nests are on tree twigs. A similar difference is seen in nests of *Ropalidia (I.) marginata* (Lepeletier) in the Northern Mariana Islands and in India. Okinawan *R. fasciata* also exhibits quite flexible social behavior, low frequency of intranidal dominance behavior, construction of satellite and multiple-comb nests, absconding swarming, and initiation and development of nests in late autumn. Study of the divergence of social habits in eusocial wasps on Pacific Islands will enhance our understanding of social evolution in insects.

THE SUBFAMILY POLISTINAE of the family Vespidae occupies a unique position in the evolution of insect eusociality, because this group has both primitively eusocial (without distinct queen-worker polymorphism) and highly eusocial (with distinct polymorphism) species. The latter are characterized by a social system with multiple queens (that is, they are “permanently polygynous” [Jeanne 1991]). This polygynous social structure is remarkably different from that of honey bees, stingless bees, and hornets (except for a few tropical species [Matsuura and Yamane 1990]), in which each colony has a single queen (Wilson 1971).

There is a debate about the evolution of such multi-queen social systems, which might reduce relatedness among nestmates (Jeanne 1991, Spradbery 1991, Itô 1993a,b). Thus, the role of kin selection (Hamilton 1964) in evolution of eusociality might be limited. West-Eberhard (1978) proposed the polygynous family hypothesis, which states that polygynous colonies of these polistine genera could have evolved from polygynous, primi-

tively eusocial groups without passing through a monogynous stage.

On the other hand, Carpenter (1991) postulated that short-term monogyny among multiple foundresses is the primitive state in the Polistinae, and single-queen and multi-queen social systems are both derived separately from this ground plan. Carpenter's argument was based on the fact that initial polygyny (multi-female founding of new nests) of primitively eusocial *Polistes* (e.g., Pardi 1942, 1946, West-Eberhard 1969), *Mischocyttarus* (Jeanne 1972), and *Ropalidia* (Gadagkar and Joshi 1983) changed to functional monogyny through dominance behavior, where only the top-ranked females could leave reproductive progeny. Carpenter defined this as “short-term monogyny.” If primitively eusocial species are found in which many colonies retain multiple egg-layers, the possibility of evolution of multi-queen systems from such species, and the polygynous family hypothesis, will have more support than at present.

Ropalidia fasciata IN JAVA AND OKINAWA

The genus *Ropalidia* is a useful subject to investigate the evolutionary process in euso-

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cial species. This large genus (136 described species found in Africa, South Asia, Australia, and Oceania) has both highly and primitively eusocial species and both monogynous and long-term polygynous (multi-queen) species (Gadagkar 1991, Jeanne 1991, Itô 1993a). The subgenus *Icarielia* includes highly eusocial, multi-queen species; the other four subgenera, including the largest subgenus, *Icariola*, are all primitively eusocial except for *R. (Icariola) ignobilis* (Saussure) (Itô 1993b). *Ropalidia* also includes independent-founding and swarm-founding species (Table 1).

Ropalidia (Icariola) fasciata (F.) occurs from India to Taiwan and Indonesia; the northern limit is the Ryukyu Islands. In Taiwan, this species constructs nests that hang from twigs of trees (Sô. Yamane, pers. comm.). In Indonesia, nests are often hung from twigs of trees and occasionally from leaves of grasses (Sô. Yamane, pers. comm.). In Okinawa, in the Ryukyu Islands, nests of this species are almost always constructed hanging from leaves of a grass, *Miscanthus sinensis* Andus., or sugarcane (Itô 1983). Although nests have been seen rarely on twigs of small trees, these were probably established by a rare, genetically different race, because females that emerged from these

nests also tended to establish their nests again on trees (unpubl. data).

Turillazzi and Turillazzi (1985) observed the social behavior of *R. fasciata* in Java and found that, in each of two postemergence nests (i.e., nests after emergence of progeny), only dominant females had developed ovaries.

In a pre-emergence nest studied by Turillazzi and Turillazzi (1985), the status of a dominant foundress was later usurped by the first progeny, whose status was usurped in turn by her younger sister. The dominant female did not perform extranidal work. Only dominant females can initiate food-requesting behavior toward returning foragers ("kiss" [Itô 1983]). Thus, in Indonesia, multi-foundress colonies changed to functionally monogynous ones through dominance hierarchy.

Although only four *R. fasciata* nests were observed by Turillazzi and Turillazzi (1985) in Java, this situation is similar to those of *R. (Icariola) marginata* (Lepeletier) in India (Gadagkar 1980, Gadagkar and Joshi 1983) and *R. (Icariola) variegata* (Smith) in Sumatra (Sô. Yamane 1986), in which the number of egg-layers was limited to one per nest except in very large nests.

In Okinawa, 55% of *R. fasciata* nests

TABLE 1

SUBGENERA OF THE GENUS *Ropalidia*

SUBGENUS	SPECIES	TYPE OF FOUNDING	TYPE OF NEST
Primitively eusocial			
<i>Icariola</i>	Most species ^a Some species ^{b,c}	Independent-founding Swarm-founding?	Arboreal nest Nonenveloped nest in cavities
<i>Ropalidia</i>	<i>maculiventris</i> Guérin ^{b,d}		Nonenveloped nest in cavities
<i>Polistratus</i>	<i>bambusae</i> Richards ^d	Swarm-founding?	Nonenveloped nest in cavities
<i>Anthreneida</i>	Some species ^e <i>sumatrae</i> (Weber) ^{b,f}	Independent-founding Swarm-founding?	Arboreal nest Nonenveloped nest in cavities
Highly eusocial			
<i>Icarielia</i>	All species ^{b,g}	Swarm-founding	Enveloped nest

^a *R. marginata* (Gadagkar and Joshi 1983), *R. fasciata* (Itô 1983), *R. revolutionalis* (Saussure) (Itô 1987).

^b Construct large colonies (> 1,000 adults) including many egg-layers.

^c *R. mackayensis* Richards and *R. trichphthalma* Richards (Jeanne 1972), *R. socialistica* (Saussure) (pers. obs.).

^d Spradbery and Kojima (1989).

^e *R. taiwana koshunensis* Sonan (Iwata 1969).

^f Aramaki (1985).

^g *R. montana* Carl (Yamane et al. 1983), *R. romandi* (Saussure) (S.-N. Shima et al., unpubl. data), *R. flavopicta* (Smith) (Sô. Yamane and K. Ikawa, unpubl. data).



FIGURE 1. Foundation of a nest by a group of foundresses of *Ropalidia fasciata* (Okinawa, 1983).

TABLE 2
 FREQUENCY OF DOMINANCE-AGGRESSIVE ACTS AMONG CO-FOUNDRESSES OF SOME POLISTINE WASPS
 (PRE-EMERGENCE PERIOD)

SPECIES	LOCALITY	n^a	NO. OF DOMINANCE ACTS	COEFFICIENT OF VARIATION	AUTHORS
<i>Polistes</i>					
<i>dominulus</i>	Italy	1	1.95		Pardi 1942
<i>canadensis</i> (L.)	Panama	6	1.36 ± 0.55	40	Itô 1985a
<i>Ropalidia</i>					
<i>fasciata</i>	Okinawa	30	0.89 ± 0.70	89	Itô 1993a
<i>gregaria</i> (Saussure)	Darwin, Australia	4	2.85 ± 0.86	30	Itô and Yamane 1992

^aNumber of observations of more than 30 min.

($n = 251$) were established by foundress groups of two to 22 individuals (Figure 1), but the frequency of dominance-aggressive behavior among co-foundresses was significantly lower than in some *Polistes* ($P < 0.05$, Mann-Whitney two-tailed U test) (Table 2).

In Okinawa, I found the following: (1) not only dominant but also subordinate females could initiate a "kiss" toward dominant and subordinate females (Itô 1983, 1985a); (2) co-foundresses coexisted on a nest until July or August, 2–3 months after the emergence of progeny females (Figure 2); (3) several females laid their eggs on these nests; and (4) at least some eggs laid by subordinates survived (Itô 1985b, 1993a).

As shown in Table 3, in *R. fasciata* even females whose status was the third rank or lower can oviposit and eat eggs laid by other females. This situation is quite different from that in *Polistes dominulus* Christ (Pardi 1942, 1946, Gervet 1964) and *P. fuscatus* (F.) (West-Eberhard 1969), where dominant females lay significantly more eggs and eat eggs laid by subordinates at a significantly higher rate, and, among subordinates, only second-rank foundresses oviposit and perform oophagy; third- or lower ranked females never perform these actions ($P < 0.05$, Fisher exact probability one-tail test) (Table 3).

Although monopolization of effective oviposition has sometimes been observed in *R. fasciata* (Kojima 1984, Iwahashi 1989), this is not a rule. Thus, the social behavior of the Okinawan population of *R. fasciata* is characterized by its great flexibility.

What causes the low frequency of dominance-aggressive acts and effective oviposition by subordinates? The survival rate of nests founded by single females was far lower than that of nests founded by multiple females. When a nest was destroyed by typhoons or predation by ants, the multi-foundress colonies reconstructed their nests, but the single-foundress colonies did not, even after emergence of some progeny (Table 4). Thus, the number of cells constructed per foundress (which was considered to be an index of fitness of the foundress) was significantly larger in nests established by six to 10 foundresses than in single-female nests, because of the high survival rate of multi-female nests ($P < 0.05$, Mann-Whitney two-tailed U test) (Figure 3).

Okinawa is famous for its frequent, strong typhoons. This may be a reason that these wasps construct their nests on grasses (grass leaves are soft and nests on these leaves are better able to survive typhoons than nests on twigs) and for the relatively peaceful coexistence of many foundresses.

Other characters of behavioral flexibility of Okinawan *R. fasciata* have been observed. Colonies often established nests with multiple combs and satellite nests (Itô 1986). The difference between multiple-comb nests and satellite nests is that in multiple-comb nests every comb was used by all colony members until the end of the colony cycle; in the latter, original nests were abandoned after establishment of satellite nests.

In addition, Okinawan *R. fasciata* col-



FIGURE 2. At least three *Ropalidia fasciata* co-foundresses (marked by arrows) were surviving on their nest 3 months after emergence of first progeny (Okinawa, 1991).

TABLE 3

OVIPOSITION AND OOPHAGY BY DOMINANT AND SUBORDINATE FEMALES IN SOME POLISTINE WASP COLONIES

SPECIES	STAGE ^a	n	OVIPOSITION BY			OOPHAGY BY		
			DOMINANT FEMALES	SUBORDINATE FEMALES ^b	% BY DOMINANT FEMALES	DOMINANT FEMALES	SUBORDINATE FEMALES	% BY DOMINANT FEMALES
<i>Ropalidia fasciata</i> ^c	Pre-	22	3	4 (4)	43	0	1	0
	Post-	22	11	10 (8)	52	1	6	14
	Total	44	14	14 (12)	50	1	7	13
<i>Polistes dominulus</i>	Pre- ^d	2	55	33 ^e	59	31	7 ^e	82
	Post- ^f	2	131	69 ^e	66	164	36	82
	Total	4	186	102 ^e	65	195	43 ^e	82
<i>Polistes fuscatus</i>	Post- ^g					41	6 ^e	87
	Pre- ^h	1	9	5 ^e	64	4	2 ^e	87

^aPre-, pre-emergence stage; post-, postemergence stage.

^bNumbers in parentheses are the mean number of eggs surviving until the end of the observation period.

^cItô (1993a).

^dPardi (1942).

^eBy second-rank females only.

^fPardi (1946).

^gGervet (1964).

^hWest-Eberhard (1969).

TABLE 4

SURVIVAL RATE OF SINGLE-FEMALE AND MULTI-FEMALE COLONIES AND NUMBER OF NESTS RECONSTRUCTED AFTER DESTRUCTION OR ABANDONMENT OF ORIGINAL NESTS IN THE OKINAWAN POPULATION OF *Ropalidia fasciata*

YEAR	% OF MULTI-FEMALE COLONIES	SURVIVAL RATE OF		NO. NESTS RECONSTRUCTED BY		
		SINGLE-FEMALE COLONY	MULTI-FEMALE COLONY	SINGLE-FEMALE COLONY	MULTI-FEMALE COLONY	UNKNOWN
1983	53.4 (58)	46.2 (26)*	86.7 (28)	0	4	1
1984	52.9 (119)	36.4 (55)*	77.8 (63)	1	3	2
1985	63.8 (47)	33.3 (15)*	88.0 (25)	0	8	9
1986	51.9 (27)	30.8 (13)*	76.9 (13)	0	1	0
Total	55.0 (251)	38.5 (109)*	81.9 (129)	1	16**	12

NOTE: Numbers in parentheses denote sample size; values for survival rate are not the same as values for percentage of multi-female colonies because some nests were sacrificed for dissection.

* Difference between values of single-female and multi-female colonies was significant ($P < 0.001$, χ^2 test).

** Difference between values of single-female and multi-female colonies was significant ($P < 0.001$, Fisher exact probability test).

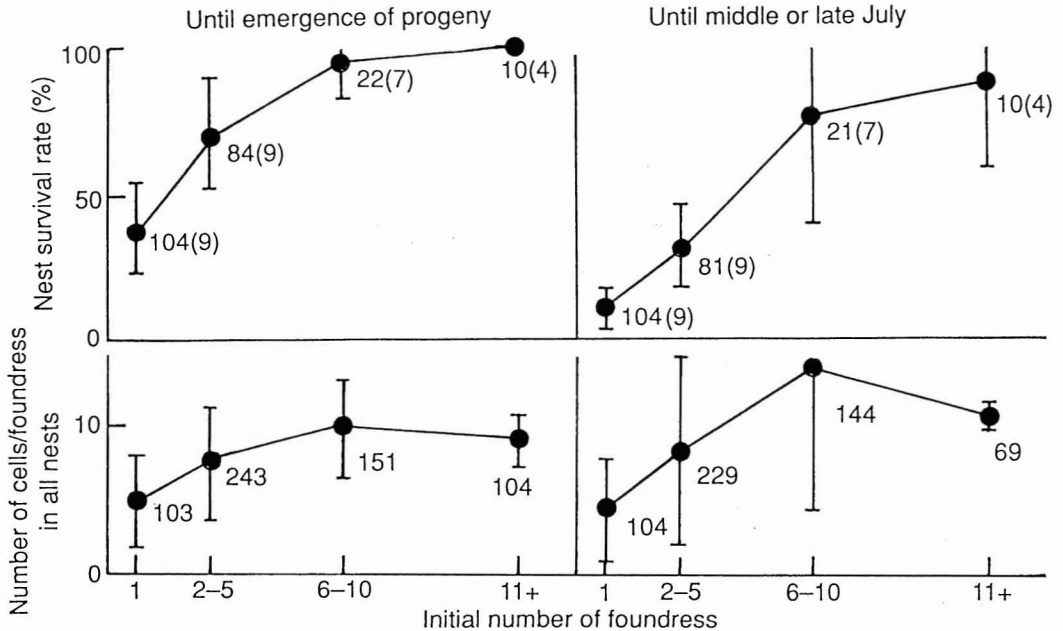


FIGURE 3. Productivity (number of nest cells constructed per foundress) and survival rate of single-female (one initial foundress) and multi-female colonies of *Ropalidia fasciata*. The numbers in the top graphs show the mean number of nests studied and, in parentheses, the number of observed cases (product of number of survey stations and years). The numbers in the bottom graphs show total number of foundresses at the initial stage of nest foundation (Okinawa, 1983–1985). Vertical lines indicate SEM.

onies often abandoned their original nests without any sign of predator attack or mechanical damage and constructed new nests (Figure 4). Before the new construction, cell contents of the original nests were removed.

This is nest relocation or absconding swarming as defined by Jeanne (1991), first reported for primitively eusocial wasps.

I also found that *R. fasciata* colonies sometimes reconstructed their nests even in

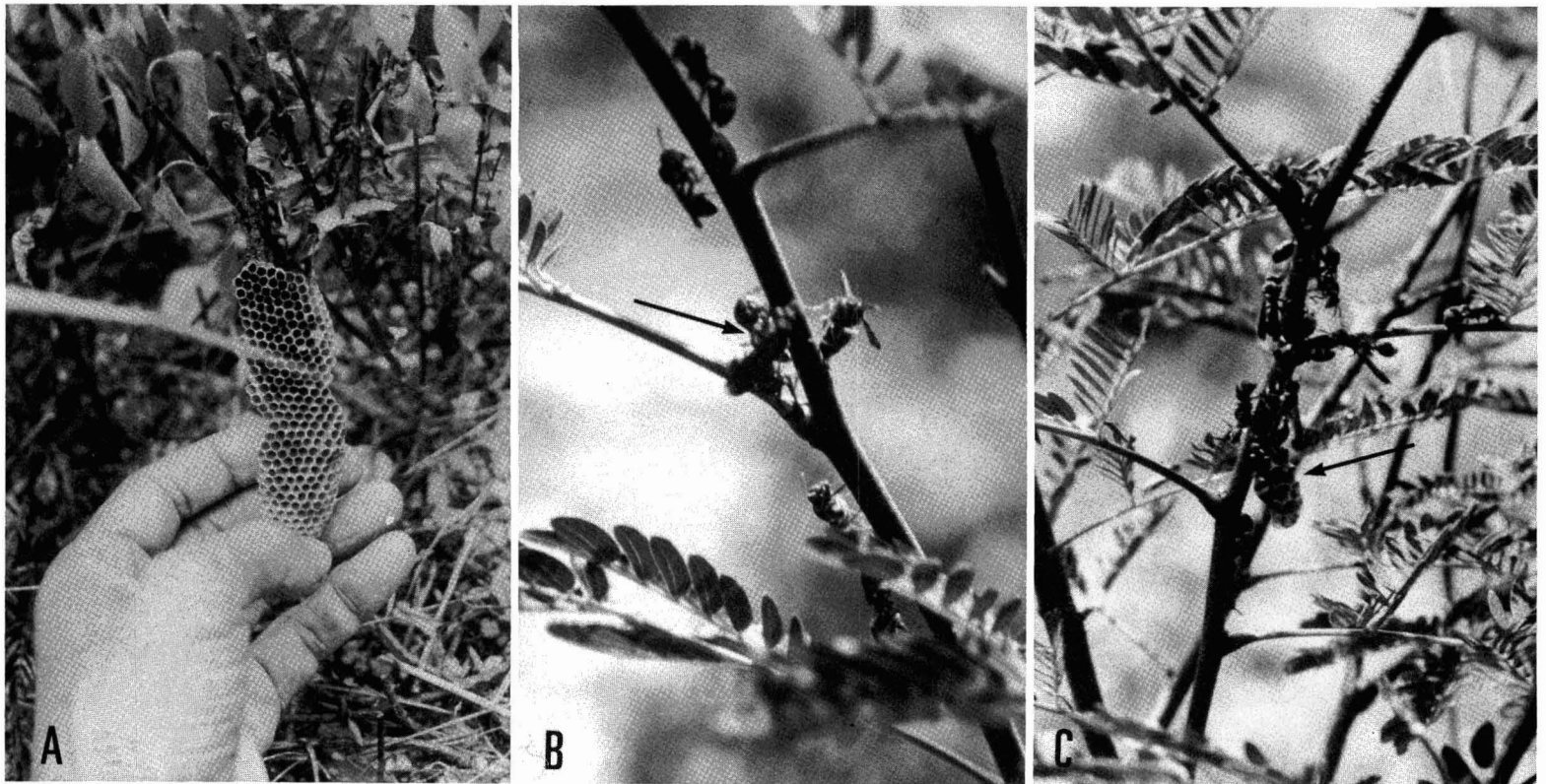


FIGURE 4. Nest relocation (absconding swarming [Jeanne 1991]) in *Ropalidia fasciata*. *A*, Original nest was abandoned after removal of cell contents (26 July). *B*, A group of females constructing a new nest (arrow) 50 cm above the original nest (26 July). *C*, The same group of females and nest (arrow) on 29 July (Okinawa, 1991).

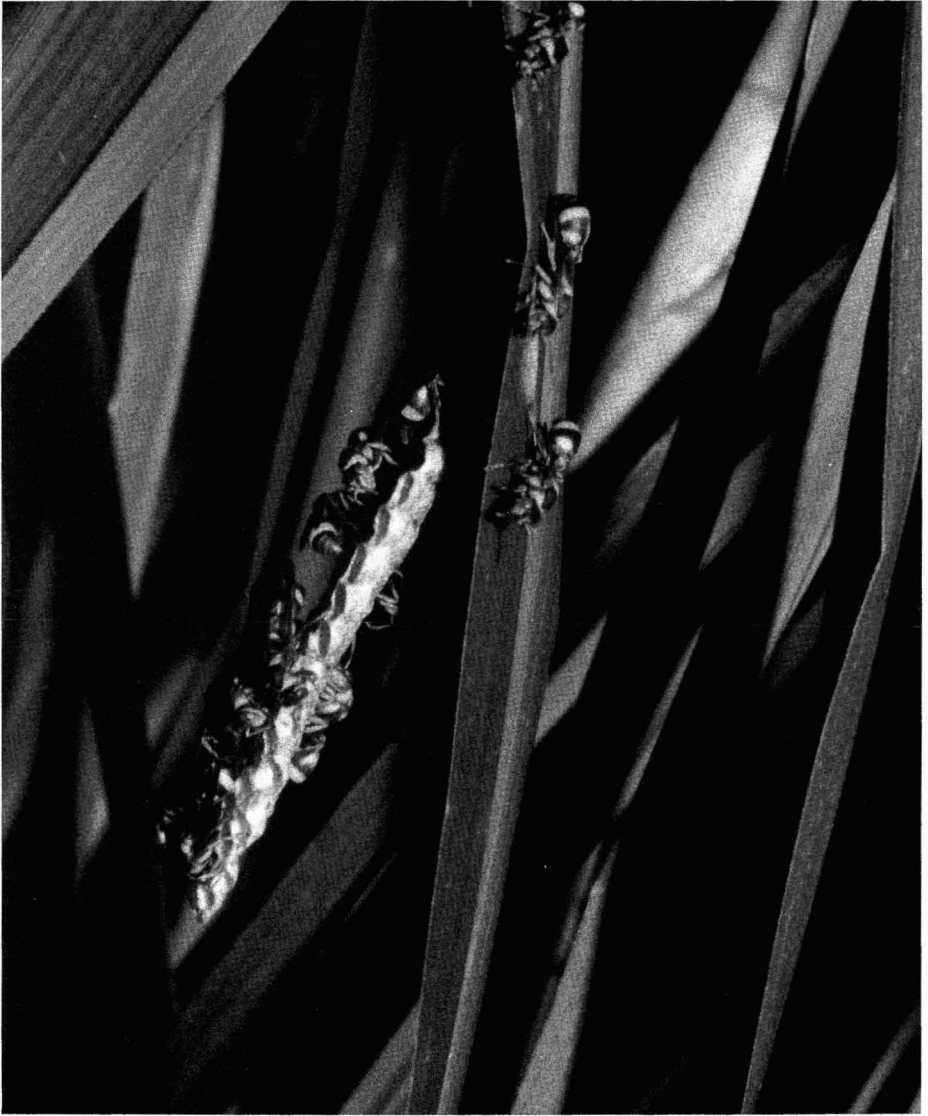


FIGURE 5. Reconstruction of a nest by progeny groups of *Ropalidia fasciata* in autumn (21 August 1992, Okinawa). No foundress was seen, but this nest produced many female progeny.

autumn (although more than 90% of the colonies complete their development in October and November). Figure 5 shows a nest being reconstructed by a large group of progeny at the end of August.

Figure 6 shows a nest established in late November. Even at this late date, not only

pupae, but also larvae and eggs were seen. This nest was still active and growing in January (Y. Sadoyama, pers. comm.). Dissection of new females taken in late November from three nests established in autumn showed that all of them were inseminated and 84% had mature ovaries. This is quite different



FIGURE 6. A *Ropalidia fasciata* nest established by four females in late November. Pupae, larvae, and eggs were seen. This nest developed until January (Okinawa, 1992–1993).

from behavior of any known *Polistes* in temperate and subtropical areas (e.g., Turillazzi 1980), in which females that emerge during autumn are inseminated but do not develop ovaries before overwintering.

These facts indicate that social behavior of Okinawan *R. fasciata* is quite flexible, possibly because of special habitat conditions on islands, especially strong predation pressure by ants and frequent typhoons. Relocation of nests by groups in *R. fasciata* is considered to be an intermediate stage between independent-founding of many *Icariola* and swarm-founding of known *Icarielia*. This suggests that the multi-queen social system of the subgenus *Icarielia* could have evolved through swarm-founding, primitively eusocial, polygynous species, as in West-Eberhard's polygynous family hypothesis.

NEED FOR STUDIES OF SOCIAL WASPS ON ISLANDS

As mentioned before, *R. marginata* shows functional monogyny in India (Gadagkar 1980, 1991, Gadagkar and Joshi 1983). This species occurs in a wide range from India to the Northern Mariana Islands and Iwo Jima of the Ogasawara (Volcano) Islands. In the Northern Mariana Islands, where typhoons are common, nests are often constructed hanging from leaves of small herbal ferns (Figure 7; S. Miyano, pers. comm.). In India, however, nests are found under eaves or on tree twigs (Figure 7). I speculate that there may be differences between the social behaviors of Marianan and Indian populations.

Two interesting species of *Ropalidia* have recently been found in Madagascar. One of

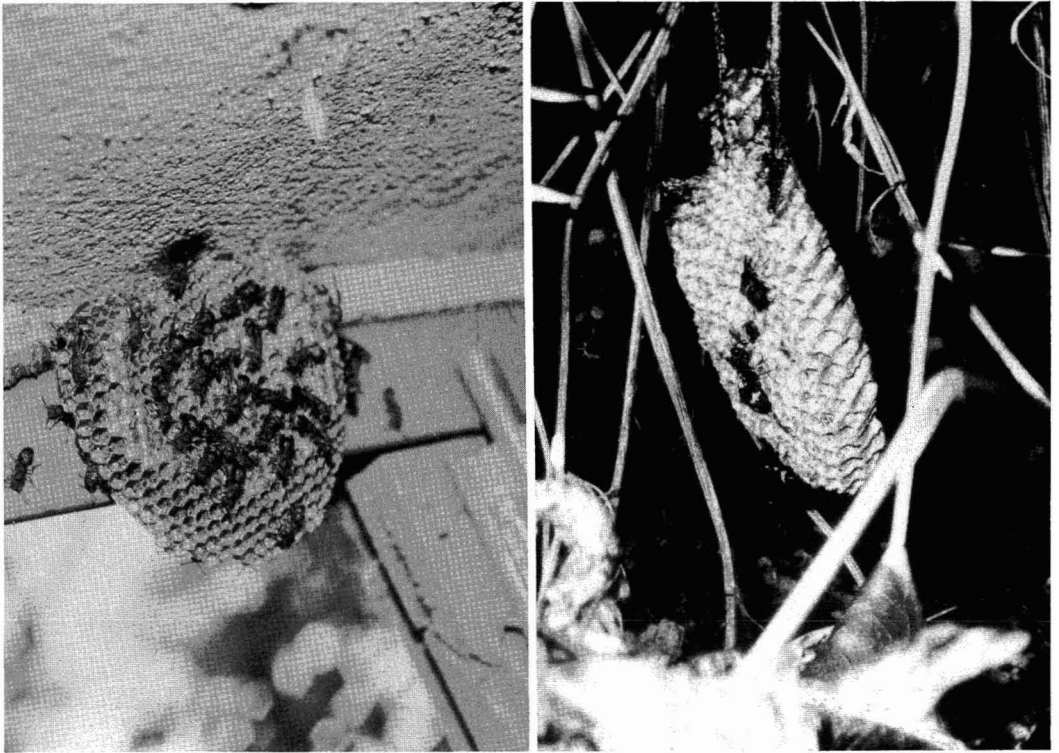


FIGURE 7. Left, A *Ropalidia marginata* nest hanging from eave of a house (Bangalore, India, 1989). Right, A *R. marginata* nest hanging from an herbal fern on Anatahan Island, Northern Mariana Islands (July 1992; photograph by S. Miyano).

them, *R. (Icariola?) formosa* (Saussure), nests gregariously, often in dense clusters of hundreds of nests under overhanging rocks (Wenzel 1987), as *R. (Icariola) plebeiana* Richards does in Australia (Itô et al. 1988). Most nests had only one adult female (mean = 1.03 females, $n = 262$) and only 10 to 20 cells (although the largest nest had 56 cells). Wenzel (1987) concluded that this is a nearly solitary species. The other species, *R. (Icariola) ignobilis*, had morphologically distinct castes despite its small colony size (Wenzel 1992). This is unique because all known highly eusocial polistine species construct large nests with hundreds of adults. Although Madagascar is far larger than Pacific Islands, founder effects and lack of competitors may affect the evolution and maintenance of such unique social characters.

Several species of another social wasp genus, North American *Polistes*, have been introduced into Hawai'i. The extent to which their behaviors have differentiated from those of mainland populations is an interesting subject for future study.

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