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Things We Don't Know About West Indian Social Wasps

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ABSTRACT
The known social wasps of the islands of the West Indies comprise 31 independent-founding and 20 swarm-founding species. Within the region, most are found only on the continental islands of Trinidad and Tobago. The present state of our nesting-biological knowledge of these 51 species is very variable. This is summarised in tabular form as a way of drawing attention to aspects that have not yet been studied. In addition, 21 scientific problems of various magnitudes are outlined. Of these, 19 have to do with social wasps in the formal sense (Vespidae: Polistinae in our area), while the other two concern members of the family Crabronidae.

INTRODUCTION

Social wasps, in the formal sense, comprise three subfamilies of the family Vespidae. Like other eusocial insects, they live in durable structured groups, known as colonies, with a reproductive division of labour. Of the approximately 700 known species in the world, 51 species, all in the subfamily Polistinae, are found in the islands of the West Indies: 38 in Trinidad & Tobago (Starr and Hook 2003) and 16 in the Antilles (Richards 1978). They fall into two major groups. In the independent-founding genera (*Mischocyttarus* and *Polistes*, known locally as Jack Spaniards), a new colony is founded by a queen or group of queens without the aid of workers. In the swarm-founders (all other genera, known as maribons or marabuntas), a colony is founded by a group of queens and workers.

Table 1 lists the social wasps of the West Indies and summarises present biological knowledge of them. My purpose here is to draw attention to 21 open questions about the biology and faunistics of these wasps. Where a statement is not referenced, it pertains to an unpublished personal observation.

1. What is the geographic source of Bocas Islands' *Polistes versicolor*?

Polistes versicolor is widespread in South America and extends into Central America (Richards 1978). It varies significantly in colouration across this range, suggesting substantial genetic variation. As a rule, in the northern part of its range the yellow marks on the body are more prominent in specimens from the western portion of its range and less so on those from the eastern portion, with an overall darkening effect. *Polistes versicolor* is one of three species of social wasps on the Bocas Islands between Trinidad and the Paria Peninsula of Venezuela. A preliminary examination suggests gene flow into the Bocas Islands from the mainland, rather than from Trinidad. This problem can possibly be satisfactorily solved through analysis of colour characters. It can certainly be solved through analysis of molecular characters.

2. Why is Tobago's social-wasp fauna so depauperate?

Trinidad and Tobago are topographically and climatically similar, differing substantially only in size; Trinidad is 16 times as large as Tobago. The general trend of the species-area relationship (Spiller and Schoener 2009) predicts that Trinidad will have about 2.5 times as many species as Tobago in a given taxon or guild. Data from a broad range of well-studied groups of plants and animals yield Trinidad/Tobago species ratios between about 2 and 5. The one exception is social wasps, of which Trinidad has 38 species and Tobago just four (Starr and Hook 2003). This case of Tobago exceptionalism calls for explanation.

3. Does Tobago have an endemic species of *Brachygastra*?

As presently conceived, *Brachygastra bilineolata* is a very widespread species, whose known range approximates South America north of the Southern Cone (Richards 1978: 172). Wasps matching the description of *B. bilineolata* are found in both Trinidad and Tobago. However, Tobago specimens are somewhat smaller and darker than those from Trinidad and the nearby mainland, suggesting an undescribed species.

4. Why is *Polistes versicolor* so prevalent on Little Tobago?

Three of Tobago's four social-wasp species are reasonably abundant on the main island. These are all swarm-founders, while the one independent-founder, *Polistes versicolor*, is rarely encountered there. On Little Tobago, in contrast, it is the most abundant species. The other species recorded from Little Tobago, *Polybia occidentalis*, is much less common, in contrast to its status as the most abundant species on both the main island and

Trinidad. We have no idea what sets Little Tobago apart in this respect.

5. Why is *Polistes dominicus* absent from Carriacou?

Polistes dominicus is present on St. Vincent and quite abundant on Union Island (8km^2) in the central Grenadines. In contrast, it is absent from Carriacou (34km^2), which is environmentally similar and just 7km to the south of Union Island. Possible explanations include: a) a subtle environmental difference that makes Carriacou less hospitable to this wasp, b) periodic local extinctions, more recently on Carriacou, without re-colonisation, and c) prevailing winds that make any southward colonization of a new island improbable. The pattern of presence and absence elsewhere in the Grenadines may throw light on this question.

6. What happened to St. Lucia's *Polistes dominicus*?

Polistes dominicus was a familiar wasp in St. Lucia within living memory, yet it has now been absent for some decades (various pers. comms.). The most commonly suggested explanation that I have heard – increased application of pesticides – is not believable, given the frequent abundance of *Polistes* spp. in other areas with much heavier pesticide use. To be plausible, any hypothesis must explain why this species is present in St. Vincent but not St. Lucia.

7. Are *Synoeca surinama* and some other species undergoing population collapse?

The global decline in amphibian numbers, suspected by herpetologists as early as 30 years ago, is now an established fact (Wake 2003). The analogous suspicion that something similar is happening to social wasps in some regions is much more recent (Dejean *et al.* 2011). A case in point in Trinidad is that of the familiar djèp tatu, *Synoeca surinama*. At least in the northern part of the island, this once common species is now hardly to be found. Some other species also seem to have become much less abundant than they were just a few years ago. What is needed, both in our region and elsewhere, is a system for field researchers to use to report on species that have become much more or less abundant in recent years.

8. What is the niche separation among Jamaican social wasps?

Jamaica has just three species of social wasps. At least in the Kingston area, *Polistes crinitus*, *P. dorsalis*, and *P. major* are all common in suburban areas, where they often nest together on buildings and other human-built structures. The niche separation between these supposedly very similar species has yet to be addressed.

9. What are the foraging ranges of *Polistes lanio* and *P. versicolor*?

Polistes lanio and *P. versicolor* are among the commonest social wasps in Trinidad. Present evidence is that the former prefers more open areas, while the latter is found in more densely vegetated areas, although there is no sharp habitat separation between the two (Kadir *et al.* 2006). What is not known is whether their foraging-flight ranges are a factor in niche separation. To begin with, we have no idea whether either species forages mostly near the nest or further afield. In the one comparable study to date, Dew and Michener (1978) found significant difference in mean flight distance between two co-occurring North American *Polistes* species.

10. What is the niche separation between *Mischocyttarus alfkenii* and *M. baconi*?

This pair of ethospecies is found in Trinidad and probably more widely in northern South America. The two species differ hardly at all physically (O'Connor *et al.* 2011), and preliminary behavioural observations show no differences aside from those leading to distinctly different nest structures (A.A. Scobie and C.K. Starr, unpubl.). Furthermore, colonies of both species are often found nesting in proximity. The niche differences that permit this coexistence will likely be more difficult to discover than in the foregoing examples of coexisting *Polistes* species.

11. Are *Angiopolybia pallens* workers attracted to smoke?

Angiopolybia pallens is the most abundant social wasp in closed-canopy forest in Trinidad. It feeds readily on fresh carrion (O'Donnell 1995; Silveira *et al.* 2005), which may be its main protein source. Preliminary observations suggest that *Angiopolybia* comes to carrion baits in especially large numbers when these are close to fire. It makes biological sense that carrion feeders should be attracted to smoke, but it is not experimentally demonstrated that they are.

12. How far away do swarm-founding species move to found?

The maximum potential colony-founding range (i.e. distance from the parent colony at which a new colony can be established) is necessarily much less for swarm-founding social wasps than it is for independent founders. However, this range has been very little studied, and we certainly do not know whether it varies systematically among species. This question has implications for population-genetic patterns and dispersal among islands. Swarming can be induced experimentally by cutting down the nest without damage to the adult wasps.

13. Does *Mischocyttarus punctatus's* nest form affect its social interactions?

While all other independent-founding social wasps in our area build a fairly compact nest comb, that of *M. punctatus* is extremely elongate, the cells almost standing end to end. This structure presumably serves as a defensive function by camouflaging the nest to resemble a vine. It has been suggested (Starr 1991) that a very elongate comb will affect social life by decreasing the frequency of one-to-one interactions among nestmates. It may also make it harder for the dominant female to maintain a reproductive monopoly. These propositions can be tested through comparison of *M. punctatus* with a sympatric *Mischocyttarus* species with a more compact nest.

14. What is the colony survivorship curve in independent-founding species?

Social-insect colonies go through a regular cycle analogous to the life cycle of individual organisms. The age-survivorship patterns of colonies can be studied in much the same way as those of individual organisms. In independent founders, the founding stage of the cycle begins at colony foundation and ends with the emergence of the first adult offspring (workers). This is presumed to be an especially hazardous period of high colony mortality (Giannotti and Machado 1994b; Reeve 1991), yet this hypothesis has been little tested. Studies of *Mischocyttarus rotundicollis* and *Polistes lanio* in Trinidad show that about half of all colonies do not survive the founding stage. What is not yet known is whether this stage occupies about half of the total cycle or significantly less or more.

15. How bang-bang is the production schedule of offspring?

Theoretical formulations lead to the prediction of an abrupt switch from producing worker brood to reproductive brood (Oster and Wilson 1978). That is, all reproductive offspring will be younger than the youngest worker. However, in North American vespine wasps Greene (1984) found substantial departure from a strict "bang-bang" pattern. In principle, it is possible to devise an index to quantify the middle ground between strict bang-bang and full overlap. In cases where the first males emerge before the first queens (protandry), examination of pupae will allow the comparative use of this index.

16. Is there age-based caste differentiation in independent-founding species?

Polymorphic workers are unknown in social wasps, but this is not to say that all workers in a colony behave alike. Newly emerged individuals are largely quiescent, and after they become active there may still be differences in their attention to different tasks. In honey bees – which also have monomorphic workers – a well-known temporal division of labour is found among workers, such that individuals shift roles as they age (Michener 1974: Table 12.3; Seeley 1995: 29-31). Nothing comparable is reported from *Mischocyttarus* or *Polistes* (e.g., Giannotti and Machado 1994a; Post *et al.* 1988), yet it seems unlikely that fully mature *Mischocyttarus* and *Polistes* workers retain the same task profiles throughout life. The small size of colonies on their open-comb nests facilitates the observation of the behaviour of workers of different ages. Marking of individuals allows them to be followed through adult life.

17. What are the threat array and sequence in our *Polistes* species?

Polistes distinguish themselves by the visual threats that they direct toward intruders at the nest. Under gradually escalating provocation, threat displays tend to originate in a species-characteristic sequence, indicative of differing release thresholds (Starr 1990). To date, these have been studied in five North American and three West Indian species (Starr 1990; C.A. Western and C.K. Starr, unpubl.). Recording the threat and array from a broader range of species can aid in analysing the comparative pattern for the genus as a whole.

18. Is there social facilitation when *Polistes* colonies attack?

If a colony is sufficiently provoked, each adult will either attack the intruder or retreat and flee from the nest. Attacking wasps do not all do so simultaneously, indicating differing individual response thresholds. Nonetheless, it often appears that many wasps attack at virtually the same instant, even without any sudden change in the provocation (R. Bhukal, unpubl.). This suggests visually-mediated social facilitation among nestmates. This would appear advantageous to the colony, but it remains to be demonstrated that it is a real phenomenon. On the other hand, no such social facilitation among fleeing wasps is predicted.

19. What is the schedule of venom expression when stinging?

The venom load and toxicity of many stinging insects has been measured, yielding estimates of the maximum capacity of individual females to deliver pain and/or tissue damage (Schmidt 1990). What is not known is whether a stinging female delivers all or most of her venom at once or only a fraction of it. Wasps are often observed to sting an intruder repeatedly in a single episode, which

suggests that not all venom is delivered in the first sting.

20. Is *Microstigmus theridii* eusocial?

Microstigmus (Crabronidae) is a Neotropical genus of 23 known species (Bohart and Menke 1976: 192; Melo and Matthews 1997). Although they are not social wasps in the formal sense, one species is known to be eusocial (Matthews 1991). All species are tiny and build simple hanging nests bound together with silk from the abdominal glands in adult females. The first species to be described, *M. theridii*, commonly has more than one adult female in a nest and so is not entirely solitary. However, it is not known whether it, too, is eusocial.

21. What is the social pattern of *Trypoxylon maidli*?

Trypoxylon (Crabronidae) is a worldwide genus of more than 359 species of mud-nesting wasps (Bohart and Menke 1976: 345-49). Most species are solitary, but some members of the *T. fabricator* group commonly have several adult females in a nest (Gobbi *et al.* 1991; Hook 2011; Matthews 1991; Sakagami *et al.* 1990). *Trypoxylon maidli* commonly nests in and on buildings in Trinidad, often with many adults sharing a nest. Nests may persist for years in sheltered locations, and preliminary observations suggest that a given nest can be utilised over a number of years. What is not known is whether cells are reutilised or if there is cooperative brood care among females.

CONCLUSION

These are of course not the only open questions about West Indian social wasps, nor are they of equal importance or difficulty. However, I believe all to be worthwhile and tractable. It is reasonable to expect that about half of them will be resolved within 10 years, giving rise to new questions.

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Table 1. Present knowledge of various aspects in the basic nesting biology of West Indian social wasps. A, nest sites. B, nest structure. C, founding-group size. D, number of effective queens in the growth stage. E, mature colony composition. F, schedule of the colony cycle. G, daily activity schedule. H, prey array. I, nest symbionts. Ref, selected references. ++, studied. +, presumably as in a closely-related studied species. It is not certain that the West Indian form of *Polybia occidentalis* is the same species as the form studied extensively in Central America.

	A	B	C	D	E	F	G	H	I	REF
Independent-Founding Species										
Mischocyttarus acunai										
M. alfkeni	++	++								
M. baconi	++	++			++					56
M. bruneri										

	A	B	C	D	E	F	G	H	I	REF
M. collarellus	++	++								62
M. cubensis		+								
M. fitzgeraldi	++	++								
M. injucundus	++	++								
M. labiatus	++	++	++	+	+					31, 34
M. metathoracicus		++								
M. mexicanus	++	++	++							7, 26, 27, 34
M. phthisicus										
M. punctatus	++	++								
M. rotundicollis	++	++			++					
M. socialis		++	+							59
M. surinamensis										
Polistes bahamensis		+						+		
P. billardieri										
P. carnifex		++								9
P. crinitus	++	++						+		61, 48
P. cubensis								+		
P. dominicus	++	++					++	+		
P. dorsalis	++	++								13
P. goeldii		++								
P. incertus										
P. lanio	++	++				++		++	++	13, 19, 21, 58
P. major	++	++								13
P. minor										
P. pacificus		++								13
P. poeyi										
P. versicolor	++	++				++		++		20, 24, 52, 48
Swarm-Founding Species										
Agelaia cajennensis		++						+		8, 38
A. multipicta	++	++						+		16, 38, 71
Angiopolybia pallens	++	++								10, 52
Apoica gelida		+			++					32, 52
A. pallens	++	+			++		++			30, 32, 52
A. pallida		++			+					52, 55
A. strigata		+			+					52

	A	B	C	D	E	F	G	H	I	REF
Brachygastra bilineolata	++	++			++					32
Chartergellus nr. *zonatus*		+			+					6, 70
Epipona tatua	++	++								42
Metapolybia cingulata	++	++			++					2, 14, 15, 32, 52
Parachartergus colobopterus	++	++		++						68
P. fraternus	++	++			++		++			32, 46
Polybia occidentalis	++	++	++	+	++	++	++	++	+	22, 28, 32, 36, 50, 52
P. quadricincta	++	++								
P. rejecta	++	++			++					32
P. striata	++	++								
P. tinctipennis										
Protopolybia exigua	++	++		+						37
Synoeca surinama	++	++	++	++	++					3-5, 32