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REVIEW

My Life as a Curious Naturalist

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1. Background

It is an honor to be invited to present an account of my career as a biologist, and I thank the editors of *Sociobiology* for this opportunity to do so. The following narrative will, I hope, give the reader an idea of the kinds of questions I like to ask and how I came to answer some of them. Many of those remain only partially answered, others completely unanswered. I call attention to some of these. Because this is more of a memoir than a topical review, I will limit citations largely to my own work and that of my students, with reference to other works where relevant; other sources will be found cited in our papers.

To explain how I got here, let me to go back to my earliest days. My mother, Ruth, was a part-time private music teacher, and my father, Armand, was a self-trained electrical engineer working at Bell Labs in New York City on the development of telephone switchboard components. Although we lived on suburban Long Island, New York, my family owned a modest summer home on 60 acres in southwestern New Hampshire. We spent our summers there, starting when I was around three years old and lasting through high school.
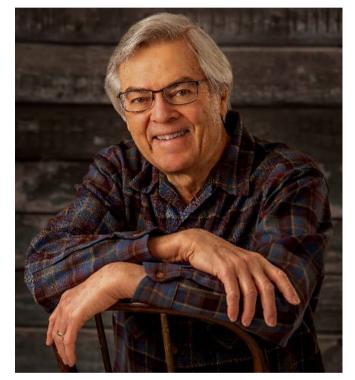

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My younger brother, Richard, and I had the run of the fields, woods, ledges, and waterways. Mom especially encouraged us to explore nature, make collections, ask questions. Those summers connected us to the natural world and made us feel comfortable in the outdoors. Spheksophobia was never a serious issue for us.

In the tenth grade I had the good fortune to have an unusually engaging teacher of biology. Harold Turkel was then a graduate student in botany at Harvard University who was teaching during the school year to support himself. He took us students on field trips to local natural areas and encouraged us to make collections, mainly of plants. His enthusiasm was contagious, so when in the fall of 1960 I enrolled as a freshman at Denison University in Granville, Ohio, without hesitation I declared a major in biology.

During my college years I took courses in botany, comparative anatomy, ecology, and more (regrettably, I could never schedule entomology!). But the class that steered me toward my future career was Bob Haubrich's course called Plant and Animal Behavior. Haubrich was another of those unusual teachers who inspire their students to see and think in new and different ways. Plant behavior was his take on plant ecology, but what most excited me were the sections on animal behavior. I always enjoyed academics and got good grades, so there was never a doubt that I would continue on to graduate school.

But first there was an interlude. In addition to meeting the requirements for the BS degree in biology at Denison, I took several classes in scientific German under Guy Stern. I recall one semester when my weekly assignment was to read and translate an article appearing in *Die Naturwissenschaften*. Back then most of the papers in that journal were in German. (The journal is now titled *The Science of Nature* and publishes exclusively in English.) Stern tipped me off to the Rotary Foundation and its scholarships in international understanding, which were designed to enable recent college graduates to study in foreign countries. With the sponsorship of the local Rotary Club, I applied and was awarded a one-year fellowship to study at the Justus Liebig-Universität in Giessen, in what was then West Germany. It was a horizon-broadening year. I attended lectures in literature, history, and even took a beginning class in Russian, taught in German. The anchoring course in biology, though, was the Zoologisches Grosspraktikum, a year-long lab course taught in the old way of a taxonomic survey. We students spent many hours each week, first learning the zoological procedures of the fixing, staining, and mounting of preserved specimens, and the use of the microscope. The second semester was devoted to drawing in intricate detail the parts of preserved animals representing all the major phyla. I became quite good at this.

While in Germany I wrote to the University of California at Berkeley and to Harvard, expressing my interest in doing graduate work in behavior. A very positive response came back from Donald Griffin at Harvard. Griffin was well-known for his discovery of echolocation in bats. His kind of research matched my interests well, so I chose to go there. Before I left Germany, however, Griffin wrote again to explain that he was leaving Harvard to go to the Rockefeller University in New York. But don't worry, he said, there was an up-and-coming young professor I could work with, and that was E. O. Wilson.

I arrived at Harvard in the fall of 1965 and quickly settled in with Wilson as my advisor. His first advice to me was to choose a taxonomic group to specialize on. Wilson, of course, worked with ants. By the end of my first semester I had narrowed my interest from the entirety of the animal kingdom down to the social insects. Meanwhile, the requirement of a reading knowledge of two foreign languages was still in place at PhD-granting institutions around the country, and Wilson personally tested his grad students' proficiencies. By the

end of my year in Giessen I was dreaming in German, so I chose to get that exam out of the way as soon as possible. For my test, Wilson opened a book by Karl von Frisch and had me translate a page. Then his telephone rang, and by the end of the 5-minute call I had the translation down pat: a pass. French was another matter. Although my immigrant paternal grandmother, who lived with us as Richard and I grew up, was a native French speaker, she taught us boys only two words: pomme de terre and moutarde. What to do? The Massachusetts Institute of Technology, on the other side of Cambridge, offered a class in French for science students, so I signed up. I did well on the midterm exam and took the result to Wilson, who said, "If it's good enough for MIT, it's good enough for me," and passed me on French. These days my reading knowledge those two languages is rarely needed. For my work, Portuguese, Spanish, and the bit of Italian I picked up later are more frequently called to duty. My Russian never made it past the eins-oh-eins class I took in Giessen.

The next step was choosing a group of social insects to focus on. It was clear to me that the ants were getting plenty of research attention, as were the honey bees, so I chose the relatively little-studied social wasps. As a graduate student developing an interest in insect ethology, I delved into the research and writings of Niko Tinbergen and Karl von Frisch, among others. I was particularly inspired by Tinbergen's four questions about animal behavior: two 'how' questions (mechanism and development) and two 'why' questions (function/adaptation and phylogenetic history) (Tinbergen, 1963). [The title of this memoir is a nod toward Niko.] Von Frisch's work on color vision in honey bees and on the function of the waggle dance were particularly inspiring examples of how well-designed experiments can quickly reveal how a given behavior works. John Platt's paper on the role of logic in designing good experiments was also influential (Platt, 1964). (See Fudge, 2014, for a 50-year retrospective.) Throughout my career, I revisited Platt from time to time and attribute my success in discovering publishable results in part to his case for the application of logic to developing hypotheses. In addition, I have always found it helpful to keep a journal in which I have conversations – and arguments – with myself about new ideas, recently published research, hypotheses I've come up with, and developing the logical pathways to experiments that can support or disprove them. Not surprisingly, in recent decades my journaling has gone digital. I have often found that when I am struggling with developing hypotheses, designing an experiment, or solving some other biological problem, if I think about it before falling asleep at night my mind will have cleared itself of other things and an insight often pops into my head. Lest it pop out again before morning, I routinely keep a pad and pen on my bedside table.

In the summer of 1966, I took the Organization for Tropical Studies course in tropical ecology in Costa Rica. It was my first introduction to the tropics. I became intrigued with tropical social wasps and did a small project on *Polistes*

at one of the research stations. That experience led to my setting my sights on tropical social wasps as a group to focus on. I selected the genus *Mischocyttarus* because it was much less known biologically than *Polistes*.

2. Toward the PhD

Back at Harvard that fall I made plans to return to Costa Rica to do the field work for my PhD dissertation. I began to learn Spanish. But in the summer of 1967, I had a chance encounter with Dr. Paulo Vanzolini, director of the Zoology Museum in São Paulo, Brazil, who at the time was visiting Harvard's Museum of Comparative Zoology (Vanzo had earned his PhD in herpetology under E. E. Williams there). He convinced me that I should really go to Brazil instead. So, I changed my plans, hurriedly learned a bit of Portuguese, and booked a flight to Belém, Pará. I still remember Ed Wilson's words of advice as I prepared to head off for months of field work: "Keep twenty irons in the fire," that is, have multiple projects on your to-do list. Some will dependably lead to results with routine data collection. These will be the meat of the dissertation. Others are more of a longshot, but those that pay off could lead to significant discovery and a paper in a major journal. Those are the gravy.

In Belém I took up residence in an apartment on the grounds of the Museu Paraense Emilio Goeldi. The Museu occupies an entire city block and is enclosed by high walls. Inside the walls are a botanic garden, a small zoo, and numerous laboratory buildings and museum collections. My plan was to study the behavior of the single most common species of *Mischocyttarus* I could find nesting on the grounds. Over the next few weeks I found numerous active nests on plants, rock walls, and buildings, and I began marking the wasps with paint spots for individual recognition, and recording their behavior on their nests. But my plan did not go well. Many of the little colonies did not last long. The grounds crew seemed to be operating under instructions to remove any wildlife that might pose harm to visitors to the grounds, and that included wasps.

So, after an unproductive few weeks I changed plans. I was able to arrange museum transportation to Utinga, a nature reserve a few kilometers outside of Belém. There I found several species of *Mischcocyttarus*, along with a variety of epiponines. Utinga afforded the protection and privacy I needed for the long-term survival of the colonies I was studying, but in the end, this did not work out either, because my rides to the preserve were only available a few days a week, and often a scheduled ride would not show up.

As the 1967 Christmas holidays approached, I took a break and travelled by bus from Belém to Brasília and then on to São Paulo, where I visited Vanzolini at the zoology museum. My most vivid memory of that time was the holiday party he hosted at his house. I remember being impressed with the diversity of the guests. They were not just colleagues from the museum, but musicians, performers, and television personalities, whom Vanzolini knew through his avocation of writing and recording samba music. Vanzo confided to me that he would never have been able to put up with a faculty position in the U.S. – too much pressure to publish, leaving no time to cultivate the rest of a life. I went on to spend New Year's eve in Rio, where I joined local celebrants to cheer as 1968 washed up onto Ipanema Beach at midnight.

I returned to Belém determined to find a better location to conduct my research, a place that had undisturbed wasp colonies right outside my door. In February, 1968, I traveled up the Amazon in search of such a site. My first stop was the field station at the Reserva Florestal Adolfo Ducke in Manaus. I spent a few days there but found the social wasp population surprisingly depauperate. What I needed was a population of at least a few nests of a single species. What I found at the Reserva was lots of species diversity, but often no more than a single colony of any one species.

Based on a suggestion from scientists at the reserve, I next took a river boat from Manaus down the Amazon to a logging camp on the Rio Curuá Una, east of the city of Santarém. My hosts were very accommodating, offering to provide me with free food and lodging should I decide to work there. But again, I found no wasp species common enough to meet my needs.

As chance would have it, on the boat from Manaus were some researchers from the museum in São Paulo. They had been tracking down and visiting localities for some of the museum's collections that had been made over the decades. One of these was Fazenda Taperinha, a plantation dating back to the 19th century that was abandoned after Brazil outlawed slavery in 1888. In the early 20th century, Gottfried Hagmann, a newly minted PhD zoologist from Switzerland, bought the place. He raised his family there and over the next decades hosted numerous botanists and zoologists who collected extensively and deposited their specimens in museums, both in Brazil and around the world. It was just upriver of the logging camp, so I hitched a ride on a barge loaded with logs heading for the mill in Santarém. They dropped me off at Santana, where I hired a boy and his canoe to paddle me up the Rio Ituquí to Taperinha.

At that time Taperinha was owned and managed by Donas Erica and Violeta Hagmann, twin daughters of the late Gottfried Hagmann. It took me just a few days to recognize that this place was ideal for what I wanted to do. One of the most abundant social wasps was *Mischocyttarus drewseni*, a large, dark species that builds fairly large nests hung from remarkably long petioles. Its nests were most common on the two main buildings on the property, but also occurred on the low vegetation scattered about the extensive grounds surrounding the houses. I had found my dream field site! Here I would do my PhD research on the social biology of *M. drewseni*. When I indicated my desire to move my field work there, the sisters welcomed me most warmly, graciously inviting me to stay as long as I wished, with free room and board.

I returned to Belém in March to tie up loose ends and prepare for the move. But first, at Vanzo's encouragement I traveled to Ribeirão Preto, São Paulo state, where Dr. Warwick Kerr invited me to stay with him and his wife while I visited his lab. I spent a couple of weeks there, looking in on all the research going on, mostly with bees at the time, and learning some of the techniques they were using. I have fond memories of my interactions with Kerr, João Camargo, and Ronaldo Zucchi, among many others.

On returning to Belém, I packed up my belongings and arrived back at Taperinha in May of 1968, to settle in for a long-term stay. I lived as a guest of the Hagmann sisters for the next year, except for a two-month hiatus in 1968, when I returned home for the last days of my father, who was dying of cancer.

The local *M. drewseni* population numbered 10-15 colonies at any one time. That was sufficient for my goal, which was a long-term intensive study of the social behavior on individual colonies. Using paint-dot-coded numbers, I marked all the adults on each colony for individual recognition, then recorded their behavior over their lifetimes. Close observation inevitably leads to questions, both Tinbergen's 'how' and 'why.' One of the most irresistible 'why' questions related to an odd and conspicuous rubbing behavior. Several times per hour the founding female would move to the top of the comb, raise her gaster, and rub the ventral side of its terminal segment up and down against the length of that long nest petiole and around its attachment to the top of the comb. On puzzling over what the function of this behavior could be, I came up with several hypotheses, some highly speculative, even outlandishly improbable. One idea was that it applied a compound that acted as an epoxy to harden the labial gland secretion that was applied to the petiole by licking. When I fastened small bits of glass microscope slide covers to the petiole and let the wasps lick them, but not rub them with the gaster, the secretion nevertheless darkened and hardened to look just like the black material of the petiole, suggesting that no second compound was needed. Meanwhile, I had noticed that small scouting-and-recruiting ants were everywhere and often approached the attachments of my nests to the substrate, but never made it down the petioles to the comb. This generated the hypothesis that the rubbing behavior served to apply an ant repellent to the petiole. The several experiments I did to test this idea provide strong support, which ultimately led to a paper in *Science* (Jeanne, 1970). Gravy. This episode reinforced for me the value of experiments that could be done in the field. Later, David Post and I went on to show the same function for the behavior in temperate-zone *Polistes* (Post & Jeanne, 1981). It has since been supported for the other three genera of independent-founding wasps.

Ed Wilson's initial letters to me while I was at Taperinha were lengthy and full of encouragement and advice. As time passed, his letters got shorter and shorter, until the last one, which said essentially, "You have enough for a PhD. Come back."

I returned to Harvard in May of 1969 to compile my results into a dissertation, which I successfully defended in late spring of 1970. The defense was a pleasant affair, Ed Wilson presiding. Not long into it, Frank Carpenter, an esteemed and congenial member of my PhD committee, sidetracked us into a discussion of insect photography, a special interest of his, and this took up most of the rest of the 45-minute meeting. I remember wondering by the end of the exam if any of my committee members had actually read my dissertation, as there were virtually no questions raised about it and little discussion of it.

Back in those times post-docs were not as all-but-required for attaining a faculty position as they are today, so after completing my degree I accepted a one-year visiting professor position in biology at the University of Virginia in Charlottesville for the 1970-1971 academic year. While handling my teaching assignments there, I revised my thesis for publication (Jeanne, 1972).

From here on in this memoir I'll organize things by topic, with apologies for demoting chronological order to second place.

3. Regulation of the colony cycle

One of the aspects of *M. drewseni*'s social life that caught my interest was the colony cycle and how it is regulated. In the relatively aseasonal environment at Taperinha, colonies are initiated in all months of the year, but last for only 5-8 months from founding to decline. I wondered why colonies decline when the environment is still benign. The queen's running out of sperm or eggs or becoming senescent were not the answer, because queens on my colonies were frequently superseded by younger females, some of them daughters of the foundress. It soon became clear that the regulation was imposed by the state of the whole colony itself. When the colony is young and the ratio of mouths to feed (Non-workers + Males + Larvae) to the rate of food supplied by workers is still low, an up-and-coming superseder will take over the colony, lay eggs, and the colony will continue to grow. Later in the cycle, with the emergence of males and non-working females (gynes), the (Nw+M+L)/Worker ratio rises, increasing the demand on the food foragers. Because the Nw and M adults get first dibs on incoming food, the larvae increasingly go unfed. As the ratio of mouths to feed vs. supplies continues to increase, even the non-worker adults are not fully fed, and they begin eating the larvae. Aspiring young dominant females have two options: (1) take over the egg-laying role from the existing queen or (2) leave and initiate their own colonies. Option (1) is not viable at this stage because of the high (Nw+M+L)/Worker ratio; any eggs they lay would be eaten. Thus, females emerging at this time are increasingly likely to leave and start (or join) new colonies, dooming their natal colony to decline.

Whether this scenario applies to other tropical independent founders, or even to swarm founders, would

make a nice comparative study. In temperate zones, the limited nesting season imposes the need for colonies to carefully time their production of gynes and males ahead of the end of the warm season. How they do this has not been fully worked out, neither for polistines nor vespines.

4. Natural Enemies and Defense

4.a. Arthropod predators

I returned to Taperinha several times in the 1970s and focused on other species that were abundant there. One of the phenomena I became curious about was the construction of multiple combs by colonies of *Polistes canadensis*. The number of combs in a mature colony can exceed 30, closely clustered together, but not touching. Most of the combs are small, averaging about 30 brood cells, and are used to rear just one generation of brood before the attending adults chew through the petiole and let the comb drop to the ground. Emptied cells are rarely reused. My pursuit of why they do all this led to a likely answer: predation on the brood by the larvae of a small tineid moth, *Antipolistes anthracella,* which appear to be attracted by the meconia in cells recently vacated by eclosing adults (Jeanne, 1979). I found that in many of the combs the moth larvae had chewed their way into neighboring occupied cells, where they fed on the larvae or pupae there. Rearing a second generation of brood in such an infested comb would be futile. Cutting and dropping them to the ground ensures that ants will make quick work of the moth larvae. This work gave rise to several questions that I was unable to address. One is why *P. canadensis* colonies in particular are attractive to *A. anthracella* when *Mischocyttarus* and other *Polistes* species in the same habitat are not. Another is whether the comb-cutting behavior is innate or is expressed only if moth larvae are detected in the cells. A third is whether the multiple combs reported for several *Polistes* spp. at scattered locations from Veracruz, Mexico, to São Paulo, Brazil, is a response to the same moth, or to different sets of natural enemies.

4.b. Ants

Working on *M. drewseni*'s defensive behavior impressed on me the importance of ants as natural enemies of social wasps, especially in the tropics. All social wasps rear their brood in open cells, subject to predation by ants. From my next faculty position (Boston University, 1971-1976) I obtained U.S. National Science Foundation funding to measure the levels of ant-predation pressure at five localities from the equator to 40° north latitude. I used live wasp larvae as baits set out in both forest and field habitats and in a variety of microhabitats in each, then recorded the rates of survival of the defenseless baits in the face of ant predation. The results showed clearly that ant predation pressure was higher in the tropics and subtropics than in the temperate zone, and that the diversity of the ant species attracted to the baits increased

markedly toward the equator (Jeanne, 1979). Although such ecological work has its own rewards, I found the 12/7 routine of checking and restocking baits and collecting ants mind-numbing. I would much prefer to sit in front of a colony of wasps observing their behavior, pondering how and why they do what they do, and dreaming up experiments to test my ideas. Yet that 1979 study is one of the most frequently cited of my papers. But then, ecology is a bigger field than is the ethology of social wasps.

In 1976 Louise Grenville Bluhm and I married, and shortly thereafter we moved to Madison, Wisconsin, where I had accepted an assistant professorship in the Department of Entomology at the University of Wisconsin. There, my graduate students and I went on to explore other aspects of defense in both tropical and temperate-zone social wasps. We pursued the chemistry of the ant repellent in *Polistes fuscatus* far enough to identify methyl palmitate as one of the active components (Post et al., 1984), work that later led to a U.S. patent for its potential as a commercial ant repellent. We also expanded our work on defensive behavior to other genera of social wasps, exploring what has turned out to be quite a diversity of mechanisms. Ant predation in particular has selected for a variety of defenses in the social wasps.

The independent-founding and the swarm-founding wasps have evolved different strategies of defense against scouting-and-recruiting ants. The former rely on repellent secretions applied to the petiole and upper parts of the comb, whereas the latter largely depend on their numerous workers for active detection and physical removal of ants that reach the nest. My graduate student Karen London showed that the evolutionary loss of chemical defense against ants was associated with the evolution of swarm founding and not the evolution of covered nests (London & Jeanne, 2000).

Army ants are a horse of a different color, able to overrun repellents, sticky traps, and even the most robust of active defenses mounted by species with some of the largest colonies. Ed Wilson referred to them as the Huns and Tartars of the insect world. Wasps that nest in association with large-colony ants such as *Azteca* spp. gain virtually complete protection against them. In the Neotropics at least 35 polistine species in 10 genera have been recorded nesting in trees occupied and defended by *Azteca*. Most of these are probably commensals, gaining protection via their hosts but providing nothing in return. An exception appears to be the mutualistic relationship entered into by *Polybia rejecta*, a notoriously aggressive wasp. It gains protection from army ants while providing protection to its host in the form of stinging attacks against ant-eating birds and mammals (Jeanne, 2021). This wasp typically nests within a few centimeters of the *Azteca* nest, close enough that it will attack birds and mammals that attempt to breach the ant nest. Such close contact is in *rejecta*'s self-interest: If they nested elsewhere in the tree it would leave the *Azteca* colony at risk of being weakened or killed by vertebrate predators, thereby exposing themselves to *Eciton* predation.

Interestingly, in the varzea (flooded-forest) habitat at Taperinha *P. rejecta* nests in tight, intraspecific clusters of up to 23 in a single small tree and not in association with any territorially dominant ant species (Jeanne, 1978). Clearly, the *Azteca-rejecta* mutualism has broken down there, but what's missing? Is it *Eciton*, or *Azteca*? Or both? The varzea and the terra firme habitats can be viewed as two naturally occurring experimental treatments, each with a distinct array of wasp predators. The two environments could be exploited to unravel some of the defensive adaptations among social wasps, and perhaps discover some new ones.

Another mode of defense against *Eciton* is nest-entrance blocking. *Synoeca septentrionalis* appears to be at least sometimes successful at this by deploying several workers to block their large entrances with their bodies. Early on at Taperinha my curiosity was aroused by *Chartergus artifex,* which narrows the inter-comb passageways in its phragmocyttarous nest to the size of a single brood cell, so that access to the upper, brood-containing combs can potentially be blocked by a single worker (Jeanne, 1991). The extremely tough outer nest carton likely prevents ants from chewing through it to gain access to the brood. The lower two or three combs have no brood cells; entrances to those combs, as well as the outer entrance, are much larger, suggesting that these chambers house a contingent of older workers that can quickly exit to defend against an attacking vertebrate. Whether these wasps actually do block the upper passageways when ants enter the nest has never been documented, but with a bit of effort one or more nests could be carefully transplanted to an area subject to army ant raids. If the colony survives unscathed after a raid passes over its nest it would be circumstantial evidence that blocking was effective. Adding ingenuity to the effort, chloroform could be injected into a nest during an army ant raid via preplaced hypodermic needles in the lower chamber (accessible to ants via the large nest entrance) and each of the next 4-5 chambers above it. Subsequent dissection of the nest would show whether ants were able to get through the narrower inner passageways and the chloroform may even freeze in place the wasp blocking the access to the brood-filled combs. With advanced technology, it may be possible to record the actual behavior during a raid via a small video camera and light placed in the lower chamber and aimed at the narrow passageway to the chamber above.

Learning plays a role in response to some ants. In *Polybia occidentalis*, for example, while recognition of the odor of *Eciton* appears to be innate, recognition of the odor of scouting-and-recruiting ants is learned upon encountering them when they attempt to invade the nest (London & Jeanne, 2005). Because the nest is often exposed to just one or two ant species occupying the shrub bearing the nest, learning their odors may enhance the speed of mounting a defense against repeated attempts to break through the wasps' defense. There is still much to be discovered about learned vs. innate recognition of the natural enemies faced by wasp species.

4.c. Parasitoids

The evolution of the nest envelope appears to have been effective in reducing the exposure of the brood not only to ants but also to parasitoids. The brood in the covered combs of the swarm-founding wasps are subject to parasitism by fewer than 25% as many species as are the independent founders, and the levels of infestation are much lower (Jeanne, 2021). Karen London showed experimentally that the envelope of *Polybia occidentalis* significantly reduces access to the brood by phorid flies, a potentially serious natural enemy (London & Jeanne, 1998). The parasitoids that do get in, such as mantispids, often have evolved indirect and intricately stealthy means of getting their propagules in past the narrow, guarded nest entrance (and getting their progeny out). These behaviors are challenging to study and have been little investigated.

4.d. Vertebrates

The first line of defense against vertebrate predators is of course the sting. The intensity of a stinging defense mounted by a colony responding to an attack on its nest varies tremendously across species and mostly correlates with species-typical colony size. But it also varies widely within species, roughly increasing with the colony's investment in the brood. While working with swarm emigration in *Polybia sericea* at Taperinha, I frequently forced active colonies to form absconding swarms by methodically dismantling their nests, comb by comb, over several minutes. Each colony pugnaciously defended its nest until all but the last one or two combs had been removed. Then, almost as if a switch had been flipped, the aggressiveness dramatically disappeared. Somehow, within seconds, the adult population had sensed that the remaining brood were no longer worth defending. But how does a colony know that its brood population has been lost and how does the information spread so quickly to and among the workers?

Karen London directly addressed the relationship between brood biomass and defense in *P. occidentalis*. She provoked newly founded colonies *P. occidentalis* to attack an artificial target in response to both mechanical and chemical (alarm pheromone) stimuli. Her results were clear: as the colonies' brood biomass grew over the 30-day pre-emergence period, the intensity of their defense increased linearly, in spite of the strong decline in numbers of workers due to post-founding attrition (London & Jeanne, 2003). Thus, the degree of a colony's defensive response is closely correlated with its investment in brood in the nest.

These results mean that a colony knows not only whether it has brood or not, it knows the current size of its investment in brood. It has recently been shown that honey bees sense the size of their worker population via the density of workers in the hive (Smith et al., 2017), but the wasp case

must involve some kind of cue or signal passed from the brood to the adults. Identifying what this is poses a fascinating challenge that we were unable to pursue. A volatile chemical emitted by the brood, a kind of "defend-me pheromone," is one possibility, but there are others. Perhaps only one stage of brood – larvae or pupae – produces the signal. Generating alternative hypotheses and designing clever experiments to disprove all but one would be a worthy PhD topic.

The nest itself may play a major role in defense against vertebrates. Just in the genus *Polybia*, for example, the species that build mud nests appear to rely on the hard structure as a first line of defense. Rather than mounting a stinging attack in the face of a mechanical disturbance, *P. emaciata* adults retreat inside, coming out to attack only after sustained disturbance. In contrast, *P. occidentalis*, which builds a flimsier carton nest, always responds to the slightest disturbance with an immediate stinging attack (O'Donnell & Jeanne, 2002). We still have little idea of the range of vertebrate predators these species face and how differences may influence selection for defensive strategies. Perhaps *P. emaciata*, which builds its ceramic-like mud nests on thin twigs and lianas, is more exposed to predation by bats (Jeanne, 1970) or small, nocturnally foraging rodents, against which a mud nest may be an effective defense.

In contrast to the many solitary wasps that build with mud, the road to eusociality in the wasps was paved with paper. Paper may initially have been an adaptation that met the need for a light and flexible nesting material that allowed the ancestor on the threshold of sociality to remove its brood comb from direct contact with the substrate by suspending it on a narrow petiole that could be defended chemically against ants. The reversion to mud, which apparently occurred twice within the genus *Polybia*, was an option available only to the lineages that lost that petiolar comb support and evolved an attachment to the substrate broad enough to support greater weight, i.e., astelocyttarous and phragmocyttarous nests. Once these architectures had evolved, a reversion to the use of mud may have been a relatively easy evolutionary step. In that regard, I once amused myself by offering small pellets of mud to *P. occidentalis* builders engaged in expanding their nest. These were accepted without hesitation and were worked into the otherwise carton nest structure. Although mud is probably cheaper to collect than wood pulp, it may require more oral section to bind it together than does wood fiber. This should be testable as part of a cost-benefit analysis of nest architectures. I'll return to the economics of nest design again in Section 9 below.

A possible example of a wasp that has evolved a way to filter its vertebrate predators is *Parachartergus colobopterus*. The color of its carton matches that of the tree trunks on which it nests, and the shallow dome of its envelope eliminates most shadows, reducing its profile for birds or bats, even from a short distance. This may narrow the range of the vertebrate predators they face to small insect-gleaning birds or mammals that forage on tree trunks. As in *P. emaciata*, when the colony

is disturbed most of the adults rush inside, while those on the outside respond to large approaching objects not by stinging, but by spraying a mist of venom at them (Jeanne & Keeping, 1995). A spritz of sticky, irritating venom in the eyes may be a more effective defense against small birds and rodents than would be one or two stings. A take-home lesson from this is that the sting's not always the thing. *Clypearia weyrauchi* has apparently independently evolved a similarly cryptic nest, but its defensive behavior has not been investigated (Jeanne, 1979).

As described above, nesting in association with other species is a common defensive adaptation of both independent – and swarm-founding wasps. *Mischocyttarus rufidens* (=*immarginatus*) often nests in close association with *Polybia occidentalis* and other swarm founders, thereby presumably gaining some protection from bird predation. We showed that founding females of *M. rufidens* nest close to their host's nest, but not so close that the nest can be reached and the brood eaten by the *occidentalis* workers (London & Jeanne, 1997). The threshold distance is about 18mm. The fact that the *rufidens* nests were not always built distally on the same twig as the *occidentalis* nests suggests that the association is maintained by vertebrate predation, not by the defense against ants provided by *occidentalis*.

Most predation on adult wasps takes place away from the nest, but the array of predators they face has been little investigated. The flying social Hymenoptera – bees and wasps – have more protein (in their flight muscles) and lipids in their bodies than do worker ants, and so may be subject to predation by a wider range of predators. Large arthropod predators such as mantids lucky enough to find a *P. occidentalis* nest can station themselves a few centimeters away from it and spend days snatching slow-flying, coming-and-going foragers with relative impunity (personal observation). On the other hand, dragonflies appear to avoid taking larger wasps, perhaps due to the risk of being stung in the neck while grasping them with their legs (Jeanne, 1972). Müllerian mimicry is common among tropical social wasps and must have evolved primarily in response to predation on foragers away from the nest. It appears to me that virtually every species of *Mischocyttarus* is a mimic of one or another sympatric epiponine wasp, but to my knowledge this has not been the subject of a systematic investigation. Selection for mimicry may come from visually hunting arthropods such as mantids, dragonflies, and jumping spiders as well as from vertebrates (O'Donnell, 1996). Any such study would need to bear in mind that the visible spectra of birds and insects differ from ours.

We know next to nothing about how nest architecture, nesting site, colony size, and other features of social wasps filter the dizzying array of predators they face. Much of the variation in nest-site selection, ferociousness of defense, body size, nest crypsis, and more may best be understood by the set of predators each species is exposed to, but has been little-explored in any rigorous, systematic way. It remains fertile ground for exploration and experimentation.

5. Communication

5.a. Swarm emigration

My last field trip to Taperinha was in 1980. Obtaining the necessary research visas and collecting permits from the Brazilian authorities had become so arduous and unreliable by then that I moved my field work to Costa Rica, starting in 1982. I found an ideal field site in Centro Ecológico La Pacífica (later Las Pumas) in the northwestern province of Guanacaste. At the time, the property was a resort, restaurant, cattle ranch, and animal rescue facility owned and operated by Werner and Lilly Hagnauer. The property was ideal habitat for *Polybia occidentalis*, which nested in abundance in the low trees dotting the pastures and along the hedgerows, so I focused much of my tropical work on that species.

I began with a study of communication. Back in 1973, while working on the ant-predation project at the Estación de Biologia Los Tuxtlas in Veracruz, Mexico, I had observed a large swarm of *Agelaia areata* on the move to a new nest site. I saw that scouts conspicuously dragged their gasters on projecting vegetation along the emigration route. Shortly thereafter Marty Naumann (1975) published his own observations of similar behavior in emigrating swarms of several other species, and speculated that its function was to deposit scent marks that guide the swarm along the route selected by scouts. A few years later, in a field experiment with *Polybia sericea* at Taperinha, I obtained experimental evidence strongly supporting the chemical trail hypothesis (Jeanne, 1981). In most species it is sternal glands that produce the trail pheromone. Yet some species lack these glands, raising the question of how they guide their swarms to new nest sites. Experimental investigation of the function of this gland in other carefully targeted species may well turn up surprising results. Chemical analysis of the products of these glands needs to be followed by bioassays done in the field to determine the active components.

Working with *P. occidentalis* in Costa Rica, Peter Sonnentag and I showed that both chemical and mechanical signals are involved in the coordination of swarm emigration. This species uses a scent-marked trail to lead the swarm to the new site. By closely observing behavior on the swarm clusters, we became proficient enough at reading early cues of the direction of the consensus nest site the scouts were converging on to locate it long before the swarm arrived. But we were primarily curious about how the scouts inform their nestmates back in the swarm that a consensus on a new site had been reached and that they should take flight and follow the chemical trail. We used videorecording of behavior at swarm clusters of *P. occidentalis* to show that returning scouts move about on the swarm surface, bumping into inactive wasps in the swarm. As the rate of bumping behavior increases, it becomes contagious, with frequently bumped swarm-mates now themselves becoming active in spreading the behavior, culminating in the swarm members taking off over several

minutes and following the scout-laid chemical trail to the new site (Sonnentag & Jeanne, 2009). We obtained information about each individual's behavior preceding her flight toward the new site by playing our videotapes backwards from her take-off. Using existing technology in innovative ways can be just as informative as applying new technology to old research problems.

Do all species of swarm-founding wasps chemically mark their emigration routes and initiate swarm emigration in the same manner? We know that *Apoica*, at least, is an exception. We found that emigrating swarms use a calling display while in flight to guide the swarm to the new nest site (Howard et al., 2002). At least two hypotheses come to mind regarding how the new site is decided on. One is that in the hours before lift-off, scouts settle on a single site, possibly marking it chemically, then guide the swarm there while keeping the wasps together in-flight via the calling pheromone. The other is that the swarm lifts off before a site has been chosen, then lands on arbitrarily selected sites a short distance away. Cleverly designed observations and/or experiments could decide between these two hypotheses – or disprove both in favor of a third I haven't thought of.

5.b. Alarm recruitment

Alarm recruitment is another context in which pheromones play a central role. At the beginning of the 1980s alarm pheromones had been demonstrated only in vespines and had been reported to be absent in the one *Polistes* species that had been tested. In 1980, in one of the last investigations I did at Taperinha, I showed experimentally that the venom of *Polybia occidentalis* contains an alarm pheromone (Jeanne, 1981). I went on to show the same for *Polistes canadensis* (Jeanne, 1982), the first for the genus. Graduate students David Post and Holly Downing later demonstrated the existence of alarm pheromones in two North American species (Post et al., 1984). In a later collaboration with a team of biochemists we identified spiroacetal (E,E)-2,8-dimethyl1,7-dioxaspiro[5.5] undecane as the active component in the venom of *P. occidentalis* and *P. sericea* (Dani et al., 2000). To my knowledge, it still has not been experimentally demonstrated that release of venom is contagious, i.e., that release by one worker elicits release by others in a chain reaction, although I provided circumstantial evidence for it in *P. occidentalis* (Landolt et al., 1998). In separate work, David Post showed that the venom of two species of *Polistes* also contains a sex pheromone that attracts males and stimulates sexual behavior (Post & Jeanne, 1983, 1984, 1985).

In some epiponine species non-pheromonal signals appear to play a role. In several species, workers in an alarmed colony move onto the envelope, or even onto the intruder, and display their flexed gasters vertically, a behavior we called gaster flagging (O'Donnell et al., 1997). In some species, the whole gaster is more conspicuously colored

than the rest of the body (in others it is just the ventrum), suggesting that the behavior has a visual-signaling function. How this adaptation functions have not been worked out. In other species mechanical signals are used to communicate alarm (see Section 5.e.).

In sum, the evidence for releasers of alarm behavior in wasps include chemical, mechanical, and possibly visual signals, and ranges from being experimentally demonstrated in a few species to speculation that needs experimental follow-up.

5.c. Foraging and recruitment to food

Sex pheromones were likely among the earliest chemical signals to evolve, no doubt long pre-dating the evolution of eusocial behavior. After sociality evolved, alarm recruitment via a chemical releaser likely soon followed. Recruitment to food sources, on the other hand, is much rarer among social species. Nevertheless, some form of trail-laying to food sources has evolved in termites, ants, and bees. Laying a chemical trail is not hard if you're a cursorial insect, but for flying Hymenoptera it's a different story. Nevertheless, the apparent failure of social vespids to evolve a similar adaptation is puzzling, given the very large colony sizes attained by some epiponine species, and that the exploitation and defense of point food sources such as carrion, utilized by a number of species, ought to favor some sort of efficient recruitment ability.

Some species of stingless bees have evolved chemical food-recruitment trails, and it doesn't seem much of a stretch to envision that the emigration-trail scent marking that is widespread in the epiponines could be commandeered for use in recruitment to food, especially in species with very large colonies. Yet so far, we have come up empty. Monica Raveret Richter, a masters student with me, showed that foragers of *Polybia sericea* use visual and chemical cues to locate prey, but she found no evidence that they recruit nestmates to food sources (Raveret Richter & Jeanne, 1985). Later, Malcolm Keeping, Jim Hunt, and I tested for recruitment to carrion in *Agelaia multipicta* and *A. hamiltoni* in Venezuela and Peru and found no evidence for it (Jeanne et al., 1995). But absence of evidence is not evidence of absence.

We later pursued the question with species more accessible to us. Several species of yellowjacket (*Dolichovespula* and *Vespula*) are common in southern Wisconsin. Stephanie Overmyer, a masters student in my lab, showed for *V. germanica* that foragers do not scent-mark rich food sources, but that naïve nestmates learn the odor of a rich food brought in by others and will leave the nest in search of its source (Overmyer & Jeanne, 1998). Jennifer Jandt, a later masters student, confirmed this and found no evidence that a behavioral signal is produced by successful foragers when they return to the nest (Jandt et al., 2005). What she did find is a cue-based recruitment system in which the odor of the food brought into the nest is alone enough to recruit others to leave

the nest and search for the source of the odor (Jandt & Jeanne, 2005). Ben Taylor, a PhD student, subsequently showed that *V. germanica* foragers search preferentially for the richer of two food resources they experience in the nest (Taylor et al., 2010). That is, resource quality matters (Taylor et al., 2012). He later showed that the rate of rhythmic gastral drumming by workers on the comb (1) increases when colonies experience an increase in the inflow of food and (2) causes increased rates of movement, trophallaxis, and departures from the nest. We concluded that gastral drumming is a nest-based recruitment signal, the first reported for a social wasp (Taylor & Jeanne, 2018).

In a series of studies in Costa Rica, Taylor and Teresa Schueller, also a PhD student, tested whether *Polybia occidentalis* has a similar nest-based food-recruitment system, and found that just as in *Vespula*, naïve foragers in the nest depart and hunt for the source of the scented resource they experienced in the nest (Schueller et al., 2010, Schueller & Jeanne, 2012, Taylor et al., 2012) and they also do not scent-mark food resources (Taylor et al., 2011).

All these species thus appear to lack off-nest signals that can guide nestmates to a rich food source, such as trail-laying, direction and/or distance-indicating dances, or even scent-marking the food source. But it would be premature to conclude from the few species investigated so far that all eusocial wasps lack off-nest food-recruitment signals. *P. occidentalis* and *V. germanica* form colonies of a just few hundred to a few thousand, at the low-to-medium range of the spectrum of colony sizes in the epiponines. Candidate species abound. One is certainly *Agelaia vicina*, with its huge colonies, but another is *Pseudopolybia difficilis*, which has an outsized Richards's gland (Jeanne et al., 1983), a tantalizing clue suggesting that it may be used to recruit to food. Such species have been waving their hands for years, in effect shouting, "Test me, test me!" Neither species occurs at my field site in Costa Rica, so the opportunity never arose.

5.d. Exocrine gland morphology

Our work with allomones and pheromones, particularly those produced by sternal glands on the gaster, led us to look into their morphology and their distribution among the social wasps. In the 1980s David Post, Holly Downing, and I published several studies of the gland histology and associated surface specializations in males and females of a number of polistine species (Jeanne & Post, 1982, Downing & Jeanne, 1983, Jeanne et al., 1983, Post & Jeanne, 1983, Downing et al., 1985). In recent years our work in this area has been expanded and improved on by others.

5.e. Vibrational signaling

As prevalent as pheromones are, mechanical signals may be equally widespread. I became aware of vibrational

signaling early on in my field work, long before Ben Taylor's discovery of the signal function of gastral drumming in *Vespula germanica*, described above. In my thesis work I described gastral drumming behavior in *M. drewseni* (I called it abdominal vibration) (Jeanne, 1972). Females drum their gasters dorso-ventrally against the nest for a fraction of a second before entering each cell to feed liquids to the resident larva. Another vibratory behavior that sometimes follows a round of feeding is what I called pecking. A female, usually the queen, would insert her head partway into a cell, then rapidly and vigorously shake her whole body forward and back longitudinally, her head contacting the cell to produce an audible rattle. At the time I had no idea of its function.

Several authors in the first half of the 20th century working with *Polistes* spp. and *Belonogaster junceus* described various forms of vibrational behavior performed while visiting larvae. Some reported that it occurred in the context of feeding liquid to larvae, while others concluded that it stimulated larvae to release their salivary secretion. In most *Polistes* species the drumming is produced by trilling the antennae on the rim of a brood cell, what we called antennal drumming. Michel Pratte and I were the first to describe in detail the form and context of antennal drumming in *Polistes* (Pratte & Jeanne, 1984). We showed that it is performed by the queen in the context of regurgitating prey liquid (imbibed while masticating prey) to the larvae and concluded that its function is to signal the larva that it is about to be fed liquid and that it should withhold the release of its salivary secretion, which is attractive to the adults. This conclusion stood for 25 years. Until we disproved it.

I began to doubt the function Pratte and I had assigned to antennal drumming when it was reported for *Polistes dominula* that vibratory behavior is performed in the same context, but only during the first half or so of the colony cycle (Brillet et al., 1999). In a 2009 book chapter I laid out additional reasons why the data don't support our salivary-inhibition idea, and to hypothesize instead that antennal drumming functions as a mechanical switch to bias the development of larvae into worker-like adults (Jeanne, 2009). The default assumption at the time was that developmental differences in social wasps are solely nutritionally based. My PhD student Sainath Suryanarayanan obtained experimental support for a role of drumming (Jeanne & Suryanarayanan, 2011, Suryanarayanan et al., 2011). Later, in a collaboration with Amy Toth at Iowa State we showed that both vibrational signals and nourishment levels experienced by developing larvae influence the expression of genes that modulate the molecular pathways related to diapause and metabolism (Jandt et al., 2017). This taught me a lesson about the need for open-mindedness and creativity when generating hypotheses – John Platt again. When Michel Pratte and I did our study in the 1980s, it simply never occurred to us that antennal drumming could have an effect on larval development. In retrospect, though, we can take some consolation from the fact that it hadn't occurred to

anyone else, either. On the plus side, I took a definite pleasure in overturning my own hypothesis, even if it took 25 years to do so. It was a good example of Karl Popper's dictum that science advances by disproof of hypotheses.

Several questions around this phenomenon remain unanswered. We speculated that the development-modulating drumming directed at the larvae may not be the only caste-influencing mechanical signals employed among the independent-founding wasps. Do the physical dominance attacks, lateral vibration, and abdominal wagging that are so widespread among the independent-founding wasps have a similar effect on gene expression that in turn influences the reproductive physiology and behavior of adult females? A study correlating level of dominance received with gene expression across individuals could answer it. Although our 2017 study showed that nourishment levels also play a role, our post-emergence treatment colonies were prevented from foraging for half the day for up to five days per week, imposing what is probably an unnaturally low food supply. Still to be determined is the relative importance of vibrational vs. nutritional inputs during the pre-emergence period. With regard to the more advanced eusocial wasps, do the vespines and the epiponines employ analogous but perhaps more subtle mechanical signals that similarly influence caste development? Or have pheromonal signals completely replaced mechanical ones?

Mechanical signals are used in contexts other than caste development. Our investigations of *Parachartergus colobopterus* showed that the species lacks an alarm pheromone, and instead workers signal alarm by drumming the tips of their gasters on the nest carton (Jeanne & Keeping, 1995). In this species not only has the venom lost its dual function of alarm pheromone and toxin to become a sticky eye irritant (described above), but the sting apparatus has evolved from a hypodermic injector into an atomizer. These changes very well may have necessitated the evolutionary change from a chemical alarm signal in the venom to a mechanical one.

Such reports are suggestive of the diversity that likely exists among the 245-odd species of Epiponini. There are two takeaways from this. One is that mechanical signals are often overlooked; not all produce sound as a byproduct. The second is that in many cases these signals may not function in ways we usually think of, that is, as releaser stimuli that elicit an immediate behavioral response, but as primers that trigger physiological changes via changes in gene expression that modify future responses to environmental stimuli or even influence developmental pathways. The science of biotremology as applied to wasps and other social insects has a wide-open future.

6. Organization of Work

My interest in this topic began after I moved my field work from Taperinha to Costa Rica and began working on

Polybia occidentalis. I became fascinated with how these colonies organize the task of nest construction. The operation involves a cooperative interaction among three groups of specializing workers: water foragers, pulp foragers, and builders. Water foragers fill their crops at a water source, then distribute their loads to pulp foragers and builders back at the nest. Pulp foragers use the water to moisten the wood source as they scrape together a pulp wad. Back at the nest, they distribute it to builders, who add it to the nest. I coined the term 'task partitioning' to describe the subdivision of resource handling into the foraging of materials in the field vs. processing them at the nest. I showed that organizing work in this way–series-parallel (Oster & Wilson, 1978) – has costs as well as benefits. The main cost arises from the need for foragers to transfer their loads to willing receivers, the builders. This can sometimes take many seconds before the forager is relieved of the last of her load, freeing her up to make her next trip. Likewise, builders face periods of idleness as they wait for the next load of water or pulp to arrive.

A major benefit of this form of task partitioning is that it allows temporal polyethism, or age specialization. Because the riskier task of foraging is performed by older workers, colonies gain a demographic advantage through an increase in the workers' mean lifespan, thus maximizing the lifetime contribution to the colony made by the average worker (Jeanne, 1986, Tofilski, 2002). Individuals make the switch from nest work to foraging suddenly and with little overlap between old and new tasks (Jeanne et al., 1988, Jeanne, 1991). The age at which workers switch from nest work to foraging ranges from 5 to 36 days of age. Part of this variability is explained by worker body size–smaller workers switch at older ages (O'Donnell & Jeanne, 1995) – and may also be influenced by lipid content (O'Donnell & Jeanne, 1995). We showed that the stinging response to a vertebrate threat, another risky task, is also performed by older workers (older than 10 days) (Jeanne et al., 1992). Methoprene, an analog of juvenile hormone (JH), when applied topically to young workers, accelerates their transition to foraging, suggesting that age polyethism is under JH control (O'Donnell & Jeanne, 1993). PhD student Cristie Roberson did a detailed study of age polyethism in *Vespula germanica* and found that it is extremely weak compared to *P. occidentalis*, despite the fact that mature colony sizes are similar in the two species (Hurd et al., 2007). This species difference still begs a coherent explanation.

Another advantage of task partitioning accrues to the foragers, who can collect and carry loads much larger than they would be able to build with on the nest. This in turn means fewer foraging trips and less foraging time per unit of material. I found that the benefit:cost ratio was higher in larger colonies, where the queuing times are reduced to a few seconds. By quantifying the number of worker-minutes it takes to collect and add one unit of nest material to the nest, I was able to show that large colonies are indeed much more efficient – in terms of worker-minutes – at nest construction

than are small ones (Jeanne, 1986). My PhD student Sean O'Donnell later showed that forager success in this species increases with experience, another benefit of specializing, since fewer individuals need to learn the location of nearby and reliable resources (O'Donnell & Jeanne, 1992).

But is the series-parallel (SP) system of organizing work seen in *P. occidentalis* actually more efficient than the parallel-series (PS) system used by the independent-founders? The latter employ little or no task partitioning when it comes to nest construction. The queen or a worker leaves the nest, flies to a place to collect water and from there to a pulp source, where she collects a small pulp load. She then returns and adds her load to the nest. Which system – SP or PS – is more efficient in terms of worker-minutes required to accomplish the same amount of work? Table 1 breaks down the components of input, in seconds, required by each of the three specialists in the SP system of *P. occidentalis* to process an average pulp-forager load (0.66mg dry wt.), resulting in a total of 1,205.6 worker-seconds.

Table 1. Series-parallel (SP) system of nest construction. For each actor (column A), the time required per task cycle (column B) is multiplied by the number of cycles (column C) of that task required to process one standard load brought in by a pulp forager. The result is the number of seconds required by that actor to service the standard load (column D). Times are in seconds and include times in queue on the nest. Data from Jeanne (1986, Table 2, large colonies).

A Actor	B Seconds per task cycle	C Multiplier (acts/mean pulp load)	D Seconds per SP unit of pulp (B x C)
Pulp forager	223.2	0	223.2
Water forager	77.5	1.35	104.6
Builder	143.9	6.1	877.8
Total			1,205.6

If *P. occidentalis* were instead to operate via the PS system of *Polistes* and *Mischocyttarus*, each worker would perform all three tasks in sequence, flying first to a water source, then a pulp source, then back to the nest to apply its load. We can again use the values I reported (Jeanne, 1986), with the following estimated (and admittedly crude) adjustments (Table 2). The size of the pulp loads the worker collects is limited by what she can build with back at the nest: 1/6.1 = 0.164 of an average *P. occidentalis* (SP) load. Likewise, she need imbibe and carry only the amount of water required to collect and build with that reduced load: 0.164, multiplied by 1.35 again, to yield 0.22 of a normal water load. Off-nest time for water foragers averaged 42.9 seconds (Jeanne, 1986, Table 2). If we assume that 10 seconds of that is required to fly to and from the source and start to collect, then 32.9 seconds is spent on water uptake. Since the PS worker needs to collect only 0.22 of an SP water specialist's load, she takes 32.9 x 0.22 = 7.2 seconds to obtain what she needs. She then flies to

Table 2. Parallel-series (PS) system. Times required if *P. occidentalis* were to use the PS system of nest construction. Tasks are performed in sequence by a forager-builder. Time at task (column B) is time off-nest for foragers and time spent building for builders (derived from data for large colonies (Jeanne, 1986, Table 2)). Columns C-F are adjustments made for the PS system. Times in seconds. See text for detailed explanation.

A Tasks (in sequence by each forager)	B Time at task	C Flying/ searching time	D Net time at task (B – C)	E Multiplier	F Flying/searching time (PS)	G Seconds per PS unit of pulp [(D x E) + F]
Water foraging	42.9	10.0	32.9	0.22	5.0	12.2
Pulp foraging	188.8	10.0	178.8	0.164	10.0	39.3
Building	61.9	0	61.9	0		61.9
Total time per trip						113.4
Adjustment to the equivalent of an SP-sized pulp load: 113.4 x 6.1						691.7

a pulp source and collects 0.164 of a normal SP load. Again subtracting 10 seconds flying/searching time to and from the pulp source from the 188.8 seconds mean off-nest time for pulp foragers leaves 178.8 for collecting the load. Again, the PS worker needs to collect only 0.164 of a load, so she spends 178.8 x 0.164 = 29.3 seconds collecting her wad and returns to the nest. Upon arrival, she builds right away; there is no transfer delay. Builders spend a mean of 61.9 seconds adding a load to the nest, which is the same for both systems, since builder-load sizes are the same. So, the total time per cycle of the PS system is 7.2 + 29.3 + 61.9 = 98.4 seconds. Adding back in 5 seconds for each of the three flights on the circuit gives 113.4 seconds. Multiplying this by 6.1 to get us back up to the full-sized SP pulp load yields 691.7 seconds (Table 2). This is much less than the 1,205.6 seconds required for the SP system because it omits the lengthy queuing times experienced by the latter. We can conclude that the PS system of the independent founders is more efficient in terms of worker-minutes than is the SP system.

If the PS system requires much less time to add a unit of pulp to the nest, what is the adaptive advantage of evolving the more time-costly SP system that appears to characterize most, if not all, of the epiponines? The answer may be that energy is the more relevant currency than is time (Jeanne, 1986). Since flight is the most energetically costly activity for social wasps, the number of foraging trips can be used as a reasonable proxy for energy expenditure. Again taking the mean dry weight of pulp collected by a *Polybia occidentalis* pulp forager (0.66mg) as a standard unit for comparison, by the SP system of *P. occidentalis*, each foraged load of pulp requires 1 trip by a pulp forager and 1.35 trips by water foragers, for a total of 2.35. The PS system, in contrast, requires 6.1 trips, or 2.6 times as many as the SP system *P. occidentalis* actually uses, and potentially 2.6 times as much energy.

There is also the demographic advantage of the SP system of *P. occidentalis*. In addition to being costly, foraging is the riskiest activity social wasps engage in. The 2.6-fold greater number of foraging trips required by the PS system exposes them to nearly a 2.6-fold increase in risk (slightly less because their trips take less time if their water and pulp sources are in the same direction from the nest). Moreover,

because there is no task partitioning, younger workers on average will be engaging in the risky task of foraging, and as explained above this will decrease workers' mean lifespan, imposing a demographic cost on the colony.

These arguments suggest that the reason task-partitioning, age polyethism, and the SP system of organizing work are adaptive is not a saving in time – there is a loss – but because they confer both energetic and demographic advantages. Whether this hypothesis holds up will require quantitative measurements of demographic and energetic costs. Among the unanswered questions are (1) why have the independent-founding wasps, especially the vespines, largely failed to evolve the SP system of organizing work? (2) Do the gains shown in *P. occidentalis* for pulp foraging (larger load size, fewer trips/mg pulp; similar for water) also occur for prey foraging? If so, does it lead to a wider range of prey sizes and types taken by swarm-founders compared to independent founders? (3) Have any of the epiponines that form extremely large colonies evolved an even more efficient way of partitioning tasks than has *P. occidentalis*? (4) Has the evolution of task partitioning and the enabling of specialists led to associated morphological/anatomical changes? For example, is the crop capacity of workers of swarm founders significantly larger, relative to body size, than among the independent founders? Crop volume can readily be measured by letting foragers imbibe water (for water foragers) or sugar water from a calibrated capillary tube (Jeanne & Taylor, 2020).

7. Evolution of Swarm Founding

In a recent paper (Jeanne, 2020) I raised the question of how swarm founding among the wasps could have evolved from independent-founding ancestors. Unlike the enormous amount of attention accorded to the origins of eusocial behavior in insects, this later step, taken at least four times in the Vespidae, has hardly been addressed. I proposed one plausible sequence of evolutionary steps. I also pointed out some of the consequences of evolving the swarm-founding mode. One of the most intriguing is that of small body size. Epiponine wasps are significantly smaller than are *Mischocyttarus* and *Polistes*. I proposed four possible hypotheses to explain this (and there

may well be others). Creative minds will come up with ways to test these. A curious aspect of the epiponine size-frequency distribution is that it is left-end truncated, i.e., there appears to be a wall at 4mm wing length below which natural selection cannot take them. I suggested that wasps smaller than this lack the size and mandible strength to collect and manipulate vegetable fibers into a nest. One testable prediction of this hypothesis is that wasps of this size construct their nests of fibers that are soft and easily collected, such as plant hairs. Undoubtedly, others will come up with additional hypotheses.

8. Colony Efficiency

My demonstration that task-integration efficiency in terms of work accomplished per worker-minute is greater in larger colonies of *P. occidentalis* (Jeanne, 1986) raised the question of whether this translates into greater overall efficiency at the colony level. My grad students and I investigated this in both *P. occidentalis* and *Parachartergus fraternus* by following growth from colony founding (by absconding swarms) to a fixed number of days just short of the emergence of the first offspring. This time frame ensured that our measures of each colony's output were solely the product of the females in the founding swarm. We measured the two forms of output: the biomass of brood in the nest and the size of the nest in weight and number of cells. When converted to per-capita productivity and regressed on colony size, the results were mixed, some datasets showing increases with colony size (Jeanne & Nordheim, 1996), while others showed no effect of colony size (Bouwma et al., 2005, Bouwma et al., 2006). Meanwhile, PhD student Kenneth Howard showed that large colonies of *P. occidentalis* rear their brood significantly faster than do small colonies (Howard & Jeanne, 2004). Taken together, these results call into serious question the dogma known as Michener's paradox, that as colonies of social Hymenoptera grow larger they become less efficient at rearing reproductives in terms of output per worker (Michener, 1964). Unlike the studies Michener analyzed, many of which used proxies that did not measure total productivity, our research explicitly set out to measure colony efficiency based on total output – the nest structure and the standing crop of brood. Several co-authors and I have recently completed a review and meta-analysis of data bearing on this issue (Jeanne et al., submitted).

Several unanswered questions arise from these results. What is the shape of the per-capita-productivity curve along an intraspecific colony-size gradient? It is probably a decelerating curve, rising to approach an asymptote, but what is that asymptote? Was it effectively reached by the larger colonies (500-600 adults) in my 1986 study, or do task-integration efficiencies continue to rise beyond that? Ken Howard's (2004) result suggests that efficiency at the colony level continues to rise through colonies of 3,000 adults. What explains those gains at the individual-performance and task-integration levels? More generally, what factors other than ergonomic efficiency select on species-specific colony size in wasps? These issues are central to such questions as the regulation of the colony cycle and how natural selection acts to determine species-specific colony size.

9. Economics of Nest Architecture

Despite all the attention devoted to nest architecture in social wasps, little has been paid to the economics of nest design. The data reported by Jeanne and Nordheim (1996) suggest that the phragmocyttarous nest of *P. occidentalis* is relatively expensive to build on a per-cell basis.
The fraction of the mass of the nest that is invested in brood cells (vs. supporting structures + envelope) is 0.29, regardless of the size of the nest. That is, the cost of adding each additional cell is the same in large and small nests. Whether this is true of all nest types remains to be determined. One advantage of the phragmocyttarous type is that nest expansion does not require tearing down any existing part of the structure, unlike in vespines and some epiponines (e.g., *Parachartergus*, *Synoeca*). Other architectural types do appear to have a much higher fraction of material invested in brood cells and are therefore cheaper to build. The gymnodomous nests of *Agelaia*, for example, have no envelope and the only supporting materials are the petioles connecting the combs. Stelocyttarous and astelocyttarous nests have non-supporting envelopes that are relatively thin and cheap. The phragmocyttarous nest type, which appears to be the most expensive to build, evolved relatively late from a stelocyttarous ancestor (Noll et al., 2020). What adaptive advantages does it confer to offset the higher cost? Details of the economics of nest type and construction behavior may help explain the evolution of nest architecture. The huge diversity of nest types among the epiponines invites a quantitative analysis of the relative economics of nest architectures.

10. Explosive Nest Construction

Another interesting aspect of nest construction is the pacing of it. In a 2004 paper Andy Bouwma and I called attention to two divergent patterns among the social wasps (Jeanne & Bouwma, 2004). The independent founders and some of the epiponines engage in continuous nest construction: the rate of cell construction is gradual and oviposition rates closely follow, leaving few if any empty cells as the nest grows. In contrast, some groups of epiponines are characterized by explosive construction: the nest is built rapidly to large size in the first days of colony founding at a pace that far exceeds the rate of oviposition, and then is not expanded for weeks or months. We proposed five factors that could favor the latter. Kevin Loope tested four of these and found support for two: first, that explosive construction minimizes exposure of the brood to natural enemies and desiccation,

and second, that rapid construction promotes competition among queens by providing a superabundance of empty cells for oviposition, thereby facilitating the selecting out of the less fecund of the multiple reproductive females (Loope & Jeanne, 2008). This is far from a settled issue. There are numerous swarm-founding polistines that do not appear to engage in explosive construction, despite being polygynous (Jeanne & Bouwma, 2004, Table 2). There is also some correlation with nest architecture: the majority of species that appear to use explosive construction build phragmocyttarous nests, compared to no phragmocyttarous nests among species engaging in continuous construction. Reaching an understanding of the adaptive advantage of explosive nest construction, its taxonomic distribution, and its correlation with nest architecture will require better data for carefully selected key species along with a new round of creative hypothesizing. As Niko Tinbergen emphasized (Tinbergen, 1963), a thorough comparative study of carefully selected species can often test among hypotheses where experimentation is not feasible. Esther Cullen's classic study of nesting adaptations in gulls remains an excellent example of the comparative approach (Cullen, 1957).

11. Regulation of Nest Construction in Epiponines

Swarm-founding wasps are complex societies (Jeanne, 2003). Their often-large worker forces specialize by age, with older individuals taking on the risky tasks of foraging and defense (see above). At a finer level, an individual worker may specialize in a way that is based on her recent experience and the current demands of her colony. Her specialization may be temporary, lasting for a few days or even just a few hours. Responses requiring the cooperation of two or more groups of specialists are self-organizing and self-regulating.

One of the most fascinating and appealing manifestations of these emergent phenomena is nest construction (NC). As described above, it requires the coordinated interaction of three groups of transitory specialists – water foragers (W), pulp foragers (P), and builders (B). For the curious biologist, the beauty of NC as a subject for investigation is that it can be activated at will simply by removing a part of the nest envelope, triggering a bout of NC to repair the damage. Moreover, most of the activity takes place in full view, where it can be videotaped.

The many questions one may ask about how NC works can be sorted into at least three categories. One focuses on the round of nest construction once it is up and running. It asks how the levels of activity of the three groups are kept in optimal proportions so as to minimize the queuing delays the workers experience during transfer of materials. The second asks what determines the overall level of the NC response. The third asks how the whole operation is started up and what brings it to a stop. Only some of these questions have ever been addressed. This is not the place for a thorough review of the subject, but I will describe two competing hypotheses on mechanism relating to the first question.

Working with *P. occidentalis,* I proposed and tested three hypotheses on the sources of information used by each of the three groups, P, B, and W, to adjust its level of activity vis à vis the others (Jeanne, 1996). I perturbed the up-and-running NC operation in two ways. First, I experimentally increased the amount of raw materials – water and wood pulp – flowing into the operation. Second, I removed some of the workers in each of the three groups in turn. I concluded that the B receive information about the nest damage directly from the nest. Feedback among B appears to determine the level of the group's building activity, which in turn sets the size of the entire repair operation, although that may be modulated downward by negative feedback from the P and W. The level of pulp-foraging activity is set by information about the demand for pulp received by P from the B. The W group similarly adjusts its activity rate in response to feedback received from P and B about the demand for water. These results support the hypothesis that information flows from the nest damage to the B and from them to the W and P; that is, information flows in a direction opposite that of the materials. Thus, it is a demand-driven operation. There is good evidence that time in queue (waiting time) to give (or receive) a building material cues information about the demand (or supply) of the material and that workers respond to the information by continuing with their task, switching to one of the other tasks, or quitting altogether.

Istvan Karsai and co-authors (Karsai & Wenzel, 2000, Karsai et al., 2020) have taken issue with this information-flow model on several grounds. One is their claim, made without explanation, that it's a runaway model. It is not. The maximum rate of NC is limited by the size of the damage being repaired. A second criticism is that I identified predetermined classes or workers identified with single behaviors. I did not. I focused on the performed tasks, not castes; the identity of the performers was secondary. A third critique is that in my model the specialists simply switch off and on instead of flexibly changing to other roles. Again, this is incorrect. Workers in each group frequently switch from one task to another; I reported this behavior in the form of transition frequencies among the three tasks (Jeanne, 1986). Karsai et al.'s fourth criticism, that they found no evidence for the feedback mechanisms I claim, is also unwarranted. I proposed and tested three explicit hypotheses on the sources of information used by P, W, and B, and provided evidence for rejecting some of them and supporting others. They provided no arguments for refuting those conclusions, performed no alternative tests leading to different conclusions from mine, nor did they put forward an alternative set of testable hypotheses. At bottom, they found no evidence in support of my model because they didn't look for any.

Karsai has proposed a somewhat more complicated model based on his observations of two species of *Metapolybia*

(Karsai & Wenzel, 2000). While *Metapolybia* colonies are typically smaller than those of *P. occidentalis*, he showed that the activity of NC is partitioned into the same three groups of tasks – P, B, and W. However, he suggested that there is a fourth worker group, a set of mostly inactive individuals on the nest that act as water tankers to provide an on-nest reservoir of water that he calls the social stomach or communal crop. (The former term is a misnomer – water is stored in the crop, not the stomach – so I will refer to this group by the latter term, abbreviated here as CC.) In support of postulating CC as a separate class, Karsai remarked that he never saw W regurgitate water directly to a P, supporting his notion that water foragers unload exclusively to the CC. In my study of *P. occidentalis* direct W-to-P transfers were a common occurrence (personal observation). I suspect that Karsai's failure to see it in his *Metapolybia* study is a result of the low rates of NC reported in his small colonies, combined with a low total number of hours of observation. His model states that the need for repair is perceived not by B inspecting the damage as in my model, but is sensed by the entire colony via the changes in light, humidity, and/or CO_2 levels caused by the removal of the envelope. W presumably begin foraging in response to the same general physical cues and unload their water to the CC group. Karsai posits that the total volume of water in the CC correlates to the size of the nest damage, and that this somehow acts as an information center to set the level of activity. That is, information flows from the nest to the CC, and then to the W, P, and B. In this sense it is a supply-driven system. In several publications (see Karsai et al., 2020, and cited papers) Karsai and co-authors have developed various computer models of the process. Left unexplained is how members of the CC group, stationed on the front of the nest (at least in *P. occidentalis*) and away from the nest damage, are better informed of the current size of the damage than are the builders (Jeanne model). It is possible that my model is correct for *Polybia* and Karsai's is correct for *Metapolybia*. I think that is unlikely.

The idea that the CC serves as a center for gathering and dispensing information about demand level adds a level of complexity to the NC system that in my view is unlikely to be adaptive. In effect, Karsai proposes a supply-driven model as an alternative to my simpler demand-driven one. Nevertheless, the Karsai proposal is a welcome addition to the effort to understand the details of how NC functions, because now there are two competing models to test. The way forward is to test predictions made by each. Mathematical models and computer simulations have their place, but they don't help us to evaluate each alternative. What's needed are observations and empirical tests on real colonies in the field. Here are a few suggestions for how to move forward on this.

1) Is the CC category real? The Karsai model predicts that members of the CC group have little or no overlap with those in the P and B task groups. The Jeanne model predicts that these workers are merely temporarily idle P and B workers who are waiting to receive enough material for their next task. Test: During ongoing NC mark members of the CC group and determine if they engage in any of the P, W, or B tasks. If not, it would support the notion of a separate fourth group, the Karsai model.

2) Who obtains the initial information about the nest damage? The Karsai model suggests that it is the whole colony; that is, the information comes in the form of changes to the physical conditions inside the nest and that no contact with the damaged parts is necessary. The Jeanne model suggests that those involved in repair – B, and perhaps P and W as well – inspect the damage directly. Test: After a day or two of marking P, W, and B as they engage in NC, allow the repairs to be completed. Early the next morning (by 6:30 or so, before NC begins and when relative humidity is high), remove a moderate amount of the nest envelope. Videorecord which marked workers inspect the damage as repair gets underway. The Jeanne model predicts it will be primarily B, perhaps P and W, but not a large contingent of unmarked workers.

3) Who takes the first step toward initiating NC at the beginning of the day? The Karsai model predicts that it starts with a good amount of water-foraging to stock the CC reservoir, then once the level approaches saturation, P and then B will begin. The Jeanne model predicts that the first foraging trip will often be by a pulp forager. On several occasions before NC begins in the early morning, I have observed that the first workers to depart the nest go to nearby leaves for water (dew), then continue on for pulp. After a short time, W become active, followed by more P as the system gains speed. This suggests that there is not a communal store of water on the nest, or the stocking of one by water foraging. Test: Same as for (2) above, but record the sequence of arrivals of water and pulp loads. If water predominates, it would support the Karsai model.

Even after these issues are resolved, others will remain to tantalize. We have a reasonable idea of how the operation responds to experimental perturbation of different kinds and this has provided clues to the sources of information used by the various groups of workers (Jeanne, 1996). What is less clear is what determines the scale of the process. I have proposed that the maximum level of NC activity is set by the amount of space available for B to work; if a B cannot find room to apply its load of pulp it is likely to quit building. The consequent feedback to P and ultimately to W in the form of fewer receivers to accept their loads will regulate the whole system slightly downward. Rates in the early mornings of the first day or two of new nest construction appear to approach this maximal level (personal observation). But it is clear that the levels of NC are often far lower. Lower levels may be imposed if the number of workers in the colony is small in relation to the size of the damage, or if the number of workers whose response thresholds are exceeded by the stimulus of the damage is small. It can also be limited by environmental conditions, notably relative humidity. We do know that NC rates slow then stop as the morning progresses, and that this

is likely due to the increasing cost per pulp load in the form of a rising W/P ratio imposed by decreasing RH (Loope & Jeanne, 2008). Cost-benefit analyses of this dynamic process have yet to be done. Then there is the question of the cues conveying the positive and negative feedback that must take place in setting activity levels. Can a builder, for example, indicate through its mouth-to-mouth contact with a nestmate that it is seeking a load of pulp and not water? Can it sense, short of contact, what a nearby nestmate has to offer? Finally, as Karsai and collaborators point out, repair work is one thing, but none of the research done so far sheds much light on how new nest construction is initiated, or how a colony decides when to expand its nest. These are questions that ought to challenge ambitious and innovative experimental naturalists. Teasing out answers will take ingenuity and persistence.

12. Conclusion

The most motivating questions for me have typically started with "I wonder why…" or "I wonder how…" Many animals, including social wasps, also show curiosity, but for them the question "I wonder what that object that just appeared over there (or on my nest) is" generally leads to one of three possible responses: chase it and/or eat it, flee from it, or mate with it. Their curiosity is largely an adaptation that enhances survival and/or reproduction. At a fundamental level it may have been the same for our ancestors: Natural selection may have favored curiosity leading to a knowledge of the natural world around them. With us moderns, it's different: We can turn a question about a particular wasp structure or behavior into a burning need to know why and how that has not the slightest connection to our surviving or reproducing – just the immense satisfaction we gain after a long, curiosity-driven pursuit of how one part of the natural world works. Paraphrasing Karl von Frisch, nature is like a magic well: the more answers we draw from it, the more questions it generates. Paraphrasing George Mallory, we sociobiologists study social insects because they're there.

I retired from the University of Wisconsin at the end of 2009, but my curiosity hasn't retired. I continue to be inspired by the wonderful diversity and intricacy of insect social behavior, and I even still publish a little bit about it every now and then.

Acknowledgments

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