SOCIAL WASP (HYMENOPTERA: VESPIDAE)
FORAGING BEHAVIOR

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Abstract Social wasps (Hymenoptera: Vespidae) forage for water, pulp, carbohydrates, and animal protein. When hunting, social wasps are opportunistic generalists and use a variety of mechanisms to locate and choose prey. Individual foragers are influenced by past foraging experience and by the presence of other foragers on resources. A forager’s ability to learn odors and landmarks, which direct its return to foraging sites, and to associate cues such as odor or leaf damage with resource availability provide the behavioral foundation for facultative specialization by individual foragers. Social wasps, by virtue of their behavior and numbers, have a large impact on other organisms by consuming them directly. Indirect effects such as disruption of prey and resource depletion may also be important. Community-level impacts are particularly apparent when wasps feed upon clumped prey vulnerable to depredation by returning foragers, or when species with large, long-lived colonies are introduced into island communities. A clearer understanding of these relationships may provide insight into impacts of generalist predators on the evolution of their prey.

OVERVIEW

In both temperate and tropical communities, social wasps (Hymenoptera: Vespidae) are often strikingly abundant. They collect water, plant fibers, and carbohydrates, and hunt arthropod prey or scavenge animal protein (28). Social wasps are generalist foragers, but individuals are able to learn and may specialize by hunting for prey or collecting other resources at specific locations (106). The foraging behavior of generalist social bees, who are able to associate the presence and quality of resources with colors, odors, shapes, and features of the environment, has greatly influenced the evolution of floral characteristics (8, 31). Similarly, the foraging behavior of generalist invertebrate predators such as social wasps, with a comparable proclivity for associative learning, may shape the evolution of their insect prey.

In this review, I summarize research on behavioral mechanisms of social wasp foraging and discuss potential ecological impacts of foraging behavior, particularly with regard to prey foraging. I report what social wasps forage for, and the
manner in which they choose and collect these resources. Interactions among wasps, via recruitment of other wasps to resources and by theft of or exclusion from resources, may be important determinants of where and how wasps forage. However, relative to recruitment to resources by eusocial bees, ants, and termites, recruitment to food is poorly developed in social wasps (65). I describe observed patterns of recruitment in these wasps and consider possible relationships between patterns of interactions among wasps and the distribution and abundance of competitors and resources.

Because social wasps are abundant components of their communities, they are likely to have considerable ecological impact (64a). Wasps may exert selective pressures on their prey, and I discuss the behavior of lepidopteran prey in relation to wasp predators. Ecological impacts of social wasps at the community level are further illustrated by examining the consequences of introducing social wasps to new environments and by documenting some examples of the use of social wasps in biological control.

Studies of social bees have been particularly fruitful in illustrating connections among ecological patterns, social systems, and behavioral mechanisms (114). Wasps, who live in a variety of ecological circumstances and exemplify a rich diversity of life histories and social systems (137), offer similar potential for productive studies on the relationship between social systems, foraging behavior, and the distribution and abundance of resources. In addition, studies of the hunting mechanisms and ecological impacts of prey foraging by social wasps may provide insight into the evolutionary importance of generalist foragers. By summarizing and synthesizing past work on the foraging behavior of social wasps from mechanistic, ecological, and evolutionary perspectives, this review is intended to serve as a catalyst for future investigations.

INTRODUCTION

Focus

The behavior and interactions of social wasps at their nests are well studied (reviewed in 112a, 137). Members of the genera Polistes (131, 134) and Mischocyttarus (58), with unenclosed colonies that are relatively easy to observe, have proven particularly popular and productive research subjects. Studies of these wasps have been a fertile source of ideas about how sociality has evolved and is maintained (5, 44, 59, 135).

Foraging behavior, especially that which takes place away from the nest at often unpredictable locations (57), is less well studied (106). Social wasps forage for water, plant fibers, protein, and carbohydrates (28). Water is imbibed by the wasps and is used in nest cooling (1, 43) and construction (64) as well as for metabolic processes. Plant fibers (pulp) are used for nest construction (133). Protein for developing brood consists of arthropod prey and, for some species, scavenged protein (1). Carbohydrate-rich foods such as nectar, sap, and fruit serve as
energy sources (117, 43). This review focuses on the basics of water, pulp, prey and carbohydrate foraging. I discuss the importance of recruitment and interactions of wasps on food and explore the impact of social wasp foraging on communities.

Phylogeny

Wasps are members of the insect order Hymenoptera, comprised of the plant-feeding suborder Symphyta and the suborder Apocrita. Apocrita contains both the parasitoid wasps and the Aculeata: stinging wasps, ants, and bees (30). Parasitoid Apocrita generally oviposit on or in arthropod hosts and may also inject a paralytic poison into hosts through their ovipositors. Aculeate wasps are believed to have evolved from a generalized parasitoid ancestor (30). The shaft of the ovipositor is modified into a sting, and the eggs of aculeate wasps leave the body through an opening at the base of the shaft. The majority of aculeate wasps use their sting to paralyze hosts more or less permanently and then carry them to a crevice or a nest where an egg is laid on the host. However, social aculeate wasps, upon which this review focuses, most often kill their prey by biting rather than stinging, and the sting is used for defense. Placement of the sting on the tip of the highly flexible metasoma enables the wasp to adeptly aim and inject venom into its foes (30).

Social aculeate wasps, with rare exception (80), are all in the family Vespidae, comprised of the subfamilies Euparagiinae, Masarinae, Eumeninae, Stenogastri- nae, Polistinae and Vespinae (17). The latter three subfamilies contain eusocial species (17) and are the focus of this review. Sociality expands the options available for finding resources and provisioning the colony. Group living makes possible behavior such as recruitment and division of labor. Different patterns of social organization among wasp species correspond to different possibilities for partitioning the tasks of locating resources and collecting, transporting, dispensing, or storing them. The following sections illustrate ways in which wasps locate, choose, and collect resources.

Water and Pulp Foraging

In addition to imbibing water or passing it along to larvae (69), social wasps mix water with masticated plant fiber in processing material for nest construction and also use water in conjunction with wing fanning in evaporative cooling of the nest (1, 43, 137). Wasps imbibe water at sources such as standing water or rain droplets on vegetation, and water is carried to the nest in the forager’s crop. At the nest, the water is regurgitated from the crop and transferred to nestmates (61). The forager may then take off from the surface of the nest and resume water collection in the field (64). Water can be a limiting resource for wasps (53). In areas or during seasons in which fresh water is scarce, social wasp foragers are frequent visitors to sinks and dripping water spigots (MA Raveret Richter, unpublished observations).
Plant fibers (reviewed in 133) such as scrapings from dead branches or weathered, unpainted wood are collected by social wasps and serve as the major structural components of their nests. In plant fiber collection by *Polybia occidentalis*, a forager lands on a piece of wood, regurgitates water from her crop onto the surface of the wood, and scrapes her mandibles across the surface of the wood until she forms a ball of pulp, which she carries in her mandibles as she flies back to her nest. Upon arriving at the nest, foragers typically transfer the pulp to nestmates and may resume foraging for additional loads of pulp (61).

Studies of the collection by *Polybia occidentalis* foragers of water and pulp for use in the task of nest construction (61, 64, 91) have provided many insights into the organization of work in social wasp colonies. The location of water and pulp in the field, at sites such as puddles, ditches, and fence posts, is somewhat more predictable than that of food resources such as prey and nectar (91). *Polybia occidentalis* foragers tend to specialize upon gathering a single type of resource, and if foragers do change from collecting one resource type to another, the switch tends to be within a functionally related group of materials: foragers more frequently switched from collecting one type of nest building material (pulp or water) to another, or one kind of food material (prey or nectar) to another, rather than switching between collecting nest building and food material (91).

In nest construction by *P. occidentalis*, pulp and water are collected by two different groups of foragers and used by a third group, the builders, in nest construction. A preliminary study (62) suggested that the rate of water collection by foragers set the pace for nest construction activity for *P. occidentalis*. However, a more recent and extensive investigation (64) suggests instead that builders respond directly to nest damage in regulating their activity. Jeanne (64) observed that the level of pulp foraging activity was a function of the demand by builders for pulp from foragers. Water foragers adjusted their foraging in response to demands for water by pulp foragers and builders. Thus, in cases where pulp and water supplies are not limited, nest construction activity was not driven by the rate at which water was delivered to the nest, but rather by the nest builders’ demand for supplies from foragers.

PREY HUNTING AND PROTEIN SCAVENGING

Solitary and Presocial Wasps

The hunting behavior of a number of solitary sphecid wasps has been studied in depth. These studies provide much of our knowledge of how wasps hunt, and several are briefly presented here as points of reference for the observations that follow on the social species. Many examples of the hunting behavior of solitary wasps are provided by Evans & West Eberhard (30) and Iwata (57). Tinbergen’s studies of *Philanthus triangulum* (129) document the responses of hunting wasps to visual and olfactory prey cues. Steiner’s (122, 123) comparisons among cricket-
hunting *Liris* and fly-hunting *Oxybelus* illustrate the characteristics and variability of hunting and prey-stinging behavior. The majority of solitary sphecid wasps are to some degree host-specific and mass-provision their young with prey such as caterpillars or bees that they have stung and paralyzed (30). Some, such as *Clypeadon laticinctus* (Hymenoptera: Sphecidae) are highly specialized and hunt only a single prey species (4).

Within the Vespidae, the solitary and presocial subfamilies Euparagiinae, Masarinae, and Eumeninae employ a variety of methods for provisioning their young (reviewed in 23). All vespids oviposit before provisioning cells (16), enabling social contact between the mother and her young in cases where the mother progressively provisions her brood (29). In the solitary Euparagiinae, comprising a single genus with nine species, young are mass-provisioned with curculionid beetles (23, 136). Most of these wasps have some degree of specificity, at least at the generic level, in prey choice (30). The subfamily Masarinae is unique among the Vespidae: These wasps feed their young a mixture of pollen and nectar and do not hunt insect prey.

In the solitary to subsocial Eumeninae, where single females nest in burrows, tubes, or free-standing mud nests (30), young are supplied primarily with stung and paralyzed caterpillar prey; a few species provision with curculionid larvae (117). Although the majority of these wasps mass-provision their brood, some are progressive provisioners, particularly at times of prey scarcity (30). The degree of prey specificity in eumenine wasps is variable (23). For example, Jennings and Housewart found differences among species and between years in the prey specificity of four conspecific eumenine wasps (66). *Ancistrocerus adiabatus* and *Ancistrocerus antilope* each provisioned with only one caterpillar species in a particular year. However, *A. adiabatus* switched from provisioning with only *Nephoteryx* sp. (Lepidoptera) in 1977 to using only *Acleris variana* (Lepidoptera) in 1978. *Ancistrocerus catskill* and *Euodynerus leucomelas* both provisioned their nests with several species of caterpillar. The caterpillar species captured differed between the two seasons, and in neither year were all cells provisioned with a single species of prey, suggesting that these wasps, similar to the social wasps to be described here, were opportunistic predators. The degrees of host specificity and constancy were influenced by changes in prey abundance and distribution in these latter wasps (66). Cowan (23) observed that, in conspecific eumenine nests, one may find one nest provisioned with a variety of caterpillar species, while the adjacent nest contains cells provisioned with a single prey species. He suggests that individual foragers may learn prey searching habits that bring them into contact with a limited range of prey, or that hunting females may return repeatedly to locations where prey are concentrated.

### Social Wasps

**Prey Specificity** Social vespids are opportunistic, generalist prey foragers (43, 106, 117). However, individual social wasp foragers often return to hunt in sites of previous hunting success (104, 108, 125, 126) and may feed repeatedly on the
same species of prey, thus functioning individually as facultative specialists (106). The choice of hunting sites can be influenced by prey density. For example, **P. jadwigae** and **P. chinensis** foragers hunting large *S. litura* (Lepidoptera: Noctuidae) larvae more frequently searched for and attacked this prey at the highest density study site (89). Thus, as with the Eumeninae described above, both past experience and the current distribution and abundance of prey appear to be important in influencing an individual’s choice of prey.

Social wasps use masticated arthropod prey and other animal protein to progressively provision their developing brood. Prey items most commonly include a variety of arthropods such as caterpillars, flies, alate ants, termites (1, 32) spiders (30, 130), bees (15, 56, 73, 79, 94, 130) and other social wasps (2, 78 as in 57, 79a). Many social wasps also scavenge vertebrate and invertebrate carrion, in addition to foraging for arthropod prey. Vespinae that scavenge protein (**V. vulgaris** species group) are notorious pests on human food, making outdoor consumption of food perilous when they are abundant (2).

Occasionally, live vertebrates are fed upon by foraging wasps and blood or tissue is collected. An imperturbable entomologist visiting British Columbia left a **V. forager** to chew on his ear, and the wasp drew blood and carried off a drop of the blood in its mouthparts (102). In Israel, **V. germanica** chewed tissue on the teats of dairy cattle, inducing mastitis in the cows (14). Grant (41) observed hornets consuming young hummingbirds, and Lacey (74) observed **Angiopterygota pellens** preying upon eggs and tadpoles in the foam nests of *Leptodactylus pentadactylus*. One response to such predation is early hatching and escape of the tadpoles. K Warkentin (personal communication) observed escape hatching of eggs of the arboreal tree frog *Agalychnis callidryas* in response to predation by **P. rejecta** foragers. Blood or tissue collection has the potential to pose serious problems for animals unable to escape or to protect vulnerable tissue from the onslaught of foraging wasps, which return repeatedly to sites at which they have foraged successfully (106).

**Prey Capture and Handling**  Wasp social organization, the regimen for provisioning brood, and environmental factors such as weather (117) and the abundance and distribution of prey (89) and predators may all influence the hunting strategies of wasps. Foragers may hunt for live prey, return to remains of prey that they have already killed, steal prey captured by other wasps (106), or scavenge carrion (2).

A hunting wasp faces several tasks. She must locate prey and distinguish it from non-food items, capture the prey, and either consume it or prepare it for transport back to the nest. While she is processing the prey, a wasp may need to protect it from other predators. Portions of prey that cannot be carried back to the nest on the first trip may need to be stowed so that they are less vulnerable to theft while the wasp is ferrying multiple loads to the nest from the capture site (109).
Live prey are generally pounced upon by social wasp foragers and killed by biting. Foragers then malaxate (process it into a ball, using the mouthparts to chew and manipulate it) the prey, carry it to the nest, and feed it progressively to their young. If prey are large and require multiple trips to carry back to the colony, a forager bites off pieces of the prey, malaxes them, carries them back to the colony, and returns quickly for the remainder of the kill. Prey remains left untended in the field are subject to theft by other hunting wasps (106) and by ants (109).

Although several authors (reviewed in 93) have documented cases in which foraging social wasps have used their sting when grappling with particularly large and active prey, the sting is generally reserved for defensive use in social wasps (3, 30). However, Olson (93) observed a *Parachartergus fraternus* forager deliver stings to the mid-abdominal segments of a stationary fourth instar *Rothschildia lebeau* (Lepidoptera: Saturniidae) caterpillar. After stinging the caterpillar, the wasp retired to nearby vegetation while the caterpillar became progressively more limp and lost its grip on the vegetation. On two separate occasions, the wasp returned to deliver an additional sting to the caterpillar. When the caterpillar had become motionless and fallen from the leaf, the wasp then began the typical malaxation of the prey. Olson (93) observed a similar incident in which a *P. fraternus* forager stung a 1.5 cm green looper caterpillar and subsequently perched on a nearby leaf while the caterpillar became limp. When the caterpillar hung motionless and was attached to the substrate only by its anal prolegs, the wasp approached and malaxed the caterpillar. Olson (93) suggests that this stinging behavior, similar to the prey stinging of non-social vespids in the Eumeninae (23), may be associated with the small mandible-length–to–body-length ratio in *P. fraternus* relative to that of other eusocial vespid genera; paralyzing the prey might better enable the wasp to process it and carry it to the nest.

Prey handling by social wasp foragers may also be influenced by the presence of allelochemicals in the host plants of their prey. Rayor et al (111) conducted tests in which paper wasp *Polistes dominulus* foragers were presented with a choice between *Pieris napi* (Lepidoptera: Pieridae) caterpillars raised on either cabbage, *Brassica oleracea*, (Brassicaceae), which contains glucosinolates, or wormseed mustard, *Erysimum cheiranthoides* (Brassicaceae), which contains both glucosinolates and cardenolides. Wasps did not detect or were not deterred by the presence of cardenolides in caterpillars raised on *E. cheiranthoides* and showed no preference for feeding on caterpillars reared upon either plant. Thus, feeding on a chemically defended host plant did not afford the caterpillars reduced predation.

Sequestration of allelochemicals from host plants can successfully reduce predation upon caterpillars by generalist hymenopteran predators such as wasps and ants (86). *Mischocyttarus flavitaris* (Hymenoptera: Vespidae) foragers reject the colored caterpillars of *Uresiphita reversalis* (Lepidoptera: Pyralidae) after superficial contact. Experimental manipulations (86) demonstrate that quinolizidine alkaloids sequestered from the host plant *Genista monspessulana* (Papilionaceae)
stored in the cuticle of *U. reversalis* caterpillars are repellent to *M. flavitarsus* foragers.

Chemical analyses demonstrated that the *Pieris napi* caterpillars in Rayor et al.’s experiments (111) did not sequester cardenolides from *E. cheiranthoides* in their tissues. Thus, when biting the mustard-fed caterpillars, wasps did not encounter high cardenolide concentrations in the epidermis or hemolymph. Upon encountering gut tissue in mustard-fed caterpillars, however, wasps contacted cardenolides. When processing these caterpillars, *P. dominulus* foragers used their mandibles to skillfully excise the gut and its contents from the balls of prey tissue they transported back to their nests. In contrast, wasps did not remove the gut from cabbage-fed caterpillars during processing. Thus, depending upon the host plant they had consumed, caterpillars were processed differently by *P. dominulus* foragers, and it took wasps significantly longer to process caterpillars fed upon wormseed mustard than those fed upon cabbage (111).

**Orientation Flights**  
Landmarks are commonly used in insect navigation (19) and help to direct the return of foraging wasps to the remains of prey too large to carry to the nest in a single load. When first departing from large prey (or other sites to which they will return), social wasps, as well as other winged Hymenoptera, perform an orientation flight. While facing the prey (109), feeder (20), nest site (28, 117) or other focal site, the wasps fly back and forth in arcs of gradually increasing radius as they increase their horizontal and vertical distance from the focus. Wasps departing from feeding sites will complete the departure flight by circling high above the ground and then flying away from the feeding site (20).

When a *Polybia sericea* Olivier forager captures prey too large to carry to the nest in one load, the forager, while facing into the wind, departs from the prey capture site flying in side-to-side arcs or circles, successively increasing its horizontal distance from the prey and at the same time ascending from 0.5 to 3.0 m above the prey; the wasp then flies to the nest (109). Wasps return to the prey capture site from downwind, facing the prey. *Polistes jadwigae* Dalla Torre (126) also make orientation flights at sites where they have killed large prey.

Field experiments demonstrate that, upon returning from downwind to the site of a past kill, *P. sericea* (105, 108) and *P. jadwigae* (126) foragers use visual landmarks to direct intensive aerial search of the foraging site; olfactory prey cues direct the forager’s landing. Displacement of the visual landmarks that had surrounded a prey capture site when a *P. sericea* forager made orientation flights significantly increased the amount of time it took for the returning forager to relocate and land upon prey remains (108).

Detailed video analyses of spatial patterning in the orientation flight of the yellowjacket *Vespula vulgaris* (20) demonstrates that these wasps orient toward and visually inspect feeders at points located toward the outermost edges of the arcs traced by the wasps during their orientation flights. They suggest that this alignment of inspection points, by providing the wasp with serial images of the goal and associated landmarks viewed at different distances, minimizes the num-
ber of views the animal must retain to steer the return to the remembered location by means of image matching, and that wasps’ landmark memories are acquired primarily during these aligned inspections. A subsequent study (18) demonstrated that for several individual foragers, the alignment of the inspection points was similar both for the departure flights and the return flights of the wasps, as would be predicted if wasps acquire landmark memories in inspection flights, and use these remembered images for orientation during the return flight.

Use of Cues in Location and Choice of Prey Foraging on natural prey often takes place infrequently at unpredictable locations, making it difficult to document how social wasps locate and choose prey in the field. Some authors have concentrated on cue use in one (58) or a few (24, 50) species, some have made generalizations across all of the vespid wasps (57), and some have pointed out the differences among different social wasps that have been studied (1).

Suggested mechanisms for how various social wasps locate and distinguish prey run a broad gamut. In early studies by Peckham and Peckham, foraging vespine wasps accumulated upon gauze bags full of chicken bones and tried to gain access to the bones; wasps did not accumulate upon control bags filled with gauze (101). This suggests that these wasps could locate food using solely olfactory cues. Iwata (57) states that olfactory cues are most important in detecting and locating prey from a distance.

Duncan (25), Frost (35), Heinrich (50), and Jeanne (58) observed wasps for which visual cues appear to determine what foragers choose to attack. Heinrich’s (50) observations on the yellowjacket Dolichovespula maculata suggest that the wasps pounce first and then discriminate between prey and non-prey; this is also suggested by the observations of Duncan (25) and Frost (35), who report the seeming lack of skill of D. maculata foragers as they repeatedly pounce upon and release nailheads and other wasps, and miss when attempting to capture flies. Jeanne (58) observed a similar method of hunting by Mischocyttarus drewseni: The wasps pounced upon nodules on plants and the barbs of barbed wire fences. Jeanne concluded that the wasps pounced in response to irregular silhouettes.

Evans & West Eberhard (30) and Raveret Richter & Jeanne (108) proposed that visual cues determine the area in which certain social wasps search intensively for prey and olfactory cues determine where a forager lands. Raveret Richter & Jeanne (108) demonstrated experimentally that Polybia sericea foragers in Brazil used visual and olfactory prey cues to relocate a foraging area and that at close range olfactory prey cues were more likely to elicit landing on stationary prey than were visual cues.

Social wasps, like bees (132), can learn to associate color (82, 116) or odor (82) with food rewards. McPheron (82) found that Mischocyttarus flavitarsis foragers learned to associate odors with rewards more quickly than they learned to associate colors with rewards. When trained to a compound (presented simultaneously) color and odor stimulus and subsequently tested for responses to indi-
vidual stimulus components, *M. flavitarsis* foragers showed a preference for odor over color.

Reflecting these learning abilities, the behavior of foraging wasps is influenced by cues that are associated with prey but do not emanate directly from the prey. Raveret Richter (105) observed that both *Polybia occidentalis* and *Polybia digitata* foragers landed preferentially on rolled or damaged leaves (more than five percent of the leaf was chewed) when foraging in a clump of low, herbaceous plants upon which leafroller larvae were feeding, suggesting that these cues might be associated with prey by foraging wasps. Cornelius (21) observed that, in choice tests conducted in a greenhouse, naive *M. flavitarsis* foragers captured more *Manduca sexta* (Lepidoptera: Sphingidae) and *Trichoplusia ni* (Lepidoptera: Noctuidae) larvae from tobacco plants with leaves previously damaged by caterpillars than from those without leaf damage. Interestingly, the wasps showed no such preference when presented with a choice of prey on damaged or undamaged tomato leaves. The presence of both visual and olfactory plant cues was necessary for the wasps to exhibit a foraging preference; neither visual nor olfactory cues by themselves elicited preferential foraging.

Additional greenhouse studies on experienced (given two days of experience in finding caterpillars on test plants prior to testing) *M. flavitarsis* (81) foraging for *T. ni* caterpillars on tomato, broccoli and bean plants demonstrated that, in contrast to Jeanne’s (58) field observations on *Mischocyttarus drewseni* in which foragers pounced on irregular silhouettes, visual prey cues (heat-cured Fimo clay caterpillar models) alone did not elicit higher frequency of approaches to or higher mean time spent hovering next to plants with green or brown caterpillar models. However, when caterpillar regurgitate was applied to brown clay models, wasps spent more time hovering near and landed more frequently upon the plants bearing these models. In the absence of visual prey cues, more time was spent hovering next to broccoli plants treated with caterpillar regurgitate relative to untreated plants. In contrast with Cornelius’s (21) work, visual cues associated with artificially induced plant damage (3 to 4 mm diameter compared to the 8 mm diameter in Cornelius’s experiment) were not associated with changes in the wasps’ foraging behavior, but leaves damaged by caterpillars were landed upon preferentially by foraging wasps. In her test of *M. flavitarsis* foragers, McPheron concluded that olfactory cues emanating from both prey and from plants damaged by caterpillars were more important than visual cues (either visual prey cues or visible plant damage) in influencing both the hovering and landing behavior of experienced foragers (81).

Hunting wasps may cue in upon chemical messages sent by other insect species and use them to locate food. Hendrichs et al (52) demonstrated that the yellow-jacket *Vespula germanica* responds to the odor of the pheromone used by Mediterranean fruit fly males, *Ceratitis capitata* (Diptera: Tephritidae), in their lek-based courtship displays. In dense foliage, where medfly leks are typically located (51), foraging wasps approached this odor from downwind and were effectively directed to aggregations of calling male flies; visual and acoustical
Social wasps collect carbohydrates from a variety of natural and anthropogenic sources, seeming to opportunistically exploit any available source of concentrated sugar (30). These carbohydrates serve as an energy source for both adults and developing brood (2). In addition to the collection of nectar from flowers, social wasps imbibe plant sap (117) and sweet liquid from fruits (30). The yellowjacket *Vespula vulgaris* collects seeds from *Trillium ovatum* Pursh. (Liliaceae), removing and consuming the carbohydrate-rich eliaosome and dispersing the seeds (68). Social wasp foragers consume honeydew excreted from plant-feeding insects such as aphids, psyllids, and coccids (71, 84, 117) and rob bees of their stored honey (30). Some social wasps collect sweet beverages and foods and can become pests at recreational areas, outdoor concession stands, and bakeries (2), where large numbers of wasps will gather and feed.

Carbohydrates are at times stored as honey in the nests of some social polistine wasps; wasp honey also serves as a source of stored amino acids (reviewed in 54). Supplementation of colonies of the paper wasp *Polistes metricus* with honey enhances brood development. This finding suggests that carbohydrate availability can be a limiting factor in wasp development (113).

Ecological data also support the idea that carbohydrates may be a critical resource for social wasp colony development. Keyel observed that natural sugar sources are often diffuse in nature (71). However, wasps able to take advantage of concentrated carbohydrate sources may build up large populations. *V. germanica*, introduced from Europe into the United States, has become abundant, replacing the native *Vespula maculifrons* in many urban and suburban habitats (88, 2). The ascendancy of this species may be in large part because of its ability to dominate rich human food sources (71, 88). Similarly, introduced vespine wasps in New Zealand have invaded the carbohydrate-rich honeydew beech forests, in which beech scale insects *Ultracoelostoma assimile* (Homoptera: Margarodidae) cover the trunks of trees and exude sweet liquid. *V. vulgaris* nest densities in the
beech forests have been recorded at 45 nests/ha, and wasp densities on scale-infested tree trunks can reach 360 insects/m², at which point tree trunks are yellow with wasps (124). These examples illustrate the potential importance of carbohydrate availability as a determinant of wasp population size.

**RECRUITMENT**

Recruitment in the context of foraging is communication that serves to bring nestmates to a food source (137). In nest-based recruitment by social insects, a solitary forager communicates the presence of a resource to other foragers at the nest (65). Simple nest-based recruitment might involve behavior such as a returning forager stimulating a group of foragers to depart from the nest merely as a result of its arrival on the nest (32). In addition, a “departure dance” (1) in which a forager runs around rapidly in the nest and is licked and antennated by nestmates prior to its return to a food source (1, 90) could further stimulate other foragers to leave the nest. Nestmates might thus be incited to forage and predisposed to visit food bearing the odor carried on the body of the recently returned or active forager. Clumped departures of wasp foragers from the nest after such a “departure dance” would provide evidence for this mechanism of nest-based social facilitation of foraging.

Although clumped departures from the nest may seem apparent to observers in the field, such clumping is difficult to demonstrate rigorously (32). Pallett & Plowright (97) contend that, despite a subjective perception that arrivals and departures from Vespula colonies appear to be clumped, quantitative analyses of contagion in departures from wasp nests (12, 27, 97) have failed to provide irrefutable evidence of this clumping. Kasuya (70) similarly found no evidence that the return of foragers to nests of Polistes chinensis antennalis stimulated nestmates to leave the nest and forage. Such clumping of departures would be consistent with social facilitation of the passage of foragers through the nest entrance or of departure from the nest (128). Existing evidence, based upon patterns of departure from the nest, is instead consistent with the interpretation that foragers arrive and depart from the nest independently. However, tests for randomness in events are sensitive to the time interval chosen, and thus the issue of independence in arrivals and departures remains unresolved (RL Jeanne, personal communication).

Social wasps in the swarm-founding Polistinae are able to use sternal gland secretions, deposited upon landmarks between the old and new nest site, to direct swarming nestmates to new nest sites (60, 63, 65). Secretions of mandibular glands are used in a similar manner by stingless bees (Meliponinae) to direct nestmates to food sources (76, 83). Swarm-founding wasps could potentially use trail pheromones, with which they direct the movement of swarms, in the context of foraging, but they are not known to do so (65). In fact, social wasps are the only group of eusocial insects (bees, wasps, ants, and termites) in which com-
munication of distance and direction to food have not been reported (63). Despite
the lack of recruitment mechanisms providing distance and direction information
to nestmates, evidence exists for some simple mechanisms of nest- and field-
based recruitment in social wasps.

Nest-Based Mechanisms of Recruitment

In studies of foraging Metapolybia azteca, M. docilis, M. cingulata, M. suffusa,
Polybia occidentalis, P. diguetana, Parachartergus fratermus, Synoeca surinama,
Brachygastera lecheguana, and Agelaia pallipes, Forsyth found no evidence of
recruitment to a specific foraging site (32). However, he stated that activity of
returning and departing foragers may stimulate other wasps to leave the nest, and
that workers grooming foragers that had just returned to the nest might obtain
odor cues that would alert them to the availability of a particular type of food.
These odor cues could serve as an important aid in food location. Naumann (90)
suggested this function for the rapid running on the nest envelope and trophal-
lactic exchanges with nestmates by returning Protopolybia pumila foragers,
although Akre (1) observes that there is no direct evidence for this interpretation.
Lindauer (76) proposed that Polybia scutellaris foragers may similarly alert nest-
mates to the presence of food. These authors suggest functional interpretations
consistent with observed behavior. However, as discussed by Jeanne et al (65),
experimental details and quantitative results are scant.

Recent work by Overmyer & Jeanne (95) provides the clearest experimental
evidence to date of a nest-based mechanism of recruitment in a social wasp. In
their study, yellowjacket (V. germanica) foragers were presented with a choice
between a dilute corn syrup solution scented the same as that being carried to the
nest by trained foragers, and a corn syrup solution bearing a different scent. Two
series of tests were conducted. In the first, vanilla was the test scent and strawberry
the control; in the second series, the odors of the training and control solutions
were reversed. In both series, foragers were significantly more likely to visit
feeders that provided the same olfactory cues as the food brought back to the nest
by the trained wasps. Unlike past studies (for example, 77), Overmyer & Jeanne
(95) controlled for the possibility of local enhancement of foraging (128), in
which foragers might be attracted to a particular resource by the actions or pres-
ence of conspecifics (discussed in 112). In Overmyer and Jeanne’s experiment
(95), naive foragers did not encounter experienced foragers at the feeders as they
approached the experimental setup. In addition, by frequently replacing the feed-
ers used in the experiments, Overmyer & Jeanne (95) controlled for the effects
of a food site marking substance deposited by feeding V. germanica (SL Overmyer
& RL Jeanne, unpublished data). Their work clearly demonstrates the existence
of nest-based, food-odor mediated recruitment of V. germanica foragers.

In contrast, experimental tests by Jeanne et al (65) on the neotropical wasp
Agelaia multipicta did not provide evidence for recruitment of foragers to carrion
in this species, either by communication of information at the nest, laying scent
trails, or by flying as a group to the foraging site, as observed by Ishay et al (56) in *Vespa orientalis*. Although their experimental protocol did not directly test for local enhancement of foraging, there was no indication that such enhancement might be occurring at the feeding site.

Field-based Mechanisms of Recruitment

Several studies have reported a tendency for social wasp foragers to distribute themselves non-randomly on carbohydrate (34, 95, 100, 110) and protein (32, 33, 106, 112) resources. Forsyth (32) suggested that the tendency of *Agelaia pallipes* foragers to accumulate on one of two identical meat baits must be due in part to visual signals, and that aggregations of foragers may be attractive because they advertise the quality of resources. SL. Overmyer & RL Jeanne (unpublished data) demonstrate that a food site marking substance is attractive to conspecific *Vespula germanica* foragers approaching unoccupied resources; odor cues emanating from or deposited by feeding wasps, in conjunction with visual cues provided by their presence, may also be an important component of forager attraction.

Parrish & Fowler observed that *Vespula germanica* and *Vespula maculifrons* foragers responded differently to carbohydrate feeders surrounded by varying numbers of a mixture of freshly killed *V. germanica* and *V. maculifrons* foragers or by hand-painted pushpins serving as odor-free wasp models (100). *Vespula germanica* foragers tended to land and feed preferentially on feeders having the highest number of pinned wasps, while *V. maculifrons* foragers preferentially avoided pinned wasps, landing on unoccupied feeders or those having the fewest pinned wasps. Similar patterns of response to the painted pushpins suggest that visual cues are sufficient to explain the observed distribution of foragers.

Parrish & Fowler (100) apply Wilson’s definition of social facilitation, “behavior initiated or increased by the action of another individual,” to the foraging behavior of the *V. germanica* foragers (137). More recent studies (96, 110, 112) suggest that local enhancement (128), a variant of social facilitation in which an animal’s attention is directed to a particular location or object by the actions or presence of conspecifics, is a more accurate descriptor of this aggregation tendency (110, 112).

In further investigations of the mechanisms involved in the discovery of food and the attraction of foragers to foraging conspecifics, Reid et al (112) observed *Vespula germanica* and *V. maculifrons* foragers scavenging on traps baited with meat. Contrary to the observations of Parrish & Fowler (100), baits upon which confined groups of conspecifics were visible were more attractive to conspecifics not only of *V. germanica* foragers, but also to *V. maculifrons* foragers, who had selectively avoided carbohydrate feeders occupied with freshly killed wasps or painted pushpins in Parrish & Fowler’s trials (100).

Reid et al (112) hypothesized that local enhancement of foraging is characteristic of wasps in the *V. vulgaris* species group. Wasps in the *V. vulgaris* species group characteristically have large, well-populated nests, and foragers have a
broad diet that includes both natural and anthropogenic resources (43); these wasps are often pests on human food. In contrast, wasps in the *V. rufa* species group have shorter colony duration and smaller colony size and are more inclined to forage on live arthropod prey and natural carbohydrate resources (43), although they will also forage at caterpillar baits (107) and honey feeders (110).

Using hexane-extracted, dried, posed wasps to provide visual cues at feeders, Raveret Richter & Tisch studied the possible role of local enhancement on carbohydrate foraging in the paper wasp *Polistes fuscatus* and in the yellowjackets *V. germanica, V. maculifrons, V. flavopilosa, V. vidua,* and *V. consobrina* (110). They compared the foraging behavior of the *Polistes* foragers with that of yellowjackets in the *V. vulgaris* (including *V. germanica, V. maculifrons,* and *V. flavopilosa* foragers) and *V. rufa* (including *V. vidua* and *V. consobrina*) species groups. Both *P. fuscatus* and *V. germanica* preferentially fed on feeders and flowers with posed wasps.

Reid et al (112) hypothesized that the ecological success of species in the *V. vulgaris* group relative to species in the *V. rufa* group is due both to their tendency to scavenge and their ability to recruit workers to scavenging sites by means of local enhancement. The preference of *V. germanica* foragers (*V. vulgaris* species group) for occupied feeders in the studies of Parish & Fowler (100) and Raveret Richter & Tisch (110) is consistent with these predictions. In the experiments of Raveret Richter & Tisch (110), where wasps visited a feeder array having both unoccupied feeders and occupied feeders on which there were unoccupied flowers, as predicted *V. germanica* visited occupied flowers on occupied feeders and fed next to the largest wasp on the feeder. Consistent with the predictions of Reid et al (112) for foragers of the *V. rufa* species group, *V. consobrina* foragers preferentially visit unoccupied feeders, and if either *V. consobrina* or *V. vidua* foragers land on occupied feeders, they preferentially visit unoccupied flowers at those feeders. However, *V. maculifrons* (*V. vulgaris* species group) foragers selectively avoided occupied feeders and flowers, consistent with the earlier results of Parrish & Fowler (100) and contrary to the predictions of Reid et al (112).

Differences between the findings of Reid et al (112) and those of other authors on the foraging behavior of wasps in the *V. vulgaris* species group may be a result of Reid et al’s (112) use of live wasps, which can move and provide odor cues, on the baits used in their tests. Other studies (100, 110) used freshly killed or hexane-extracted pinned wasps or models in which all visual cues were stationary, and odor was not always present. Stationary visual cues may be sufficient for local enhancement in *V. germanica* foragers, but may elicit avoidance by *V. maculifrons* foragers. Scale may also be important: *V. maculifrons* foragers avoided other foragers when foraging on a large array, but showed local enhancement of foraging when presented with a choice among only two or three closely spaced feeders (discussed in 110). Geographic or population level differences may underlie these behavioral differences (RL Jeanne, personal communication). The studies of Reid et al (112) were conducted in the Midwest, while those of Parrish & Fowler (100) and Raveret Richter & Tisch (110) were conducted on the East
Coast of the United States. Finally, Reid et al (112) used protein baits in their studies, whereas all of the work demonstrating local enhancement of *V. maculifrons* foragers used carbohydrate baits—foragers may behave differently on different types of resources.

Keyel (71) suggested that the ability of the introduced *V. germanica* to monopolize resources, despite the fact that these wasps are displaced from resources in one-on-one encounters with native *V. maculifrons* and *V. flavopilosa* foragers, is due to their tendency for local enhancement. *V. germanica* foragers are recruited to a resource more rapidly than are *V. maculifrons* or *V. flavopilosa* foragers. Once present, *V. germanica* foragers are able to maintain control of the site because of their increased tendency to grapple with intruders at resources.

**Why is Recruitment Poorly Developed in Social Wasps?**

Compared to the behavior of other social insects, the recruitment of social wasps to resources is poorly developed. Despite possession of mechanisms, such as trail pheromones (60), that could enable communication of distance and direction information, and despite the potential advantages that could accrue from efficient recruitment of nestmates directly to specific locations, social wasps do not recruit. They remain the only group of eusocial insects in which communication of distance and direction to food have not been reported (63). Even less sophisticated forms of recruitment, such as local enhancement, are not necessarily the norm. Many wasp species (106, 110) preferentially avoid occupied resources. The question, then, is why aren’t social wasps more inclined to recruit? Jeanne et al (65) reviewed some possible explanations, including social constraints on recruitment (is it necessary to pass a threshold colony size in order to make recruitment profitable?), lack of ability to store proteinaceous food (might social wasp species that store nectar recruit to carbohydrate sources?), and the influence of ecological factors.

Ecological factors including the distribution and abundance of resources, competitors, and predators are likely to be important determinants of foraging strategies. For example, recruitment activities, because of the time involved, could leave resources undefended for extended periods of time. If resources are generally of a size that can be carried back to the nest by an individual in a few trips, those resources might be most efficiently harvested—and left unattended and vulnerable to theft at the capture site for the least amount of time—if a forager were to gather a load, carry it to the nest, quickly hand off her load to a nestmate, and immediately return to the resource in the field (106, 109). A forager’s ability to learn, during an orientation flight, the landmarks associated with the location of the resource (18) enables her to return to a resource efficiently.

Very large resources present the wasps with stiff competition from able recruiters such as ants and stingless bees, and ants may also pose a predation risk for the wasps (65). Mobilizing groups of wasps large enough to hold off these foes would make the wasps, clumped offensively or defensively on resources, less
able to disperse themselves widely over the landscape, and thus less likely to encounter new resources. In discussing the foraging strategies of *Trigona* bees, Johnson (67) reasoned that opportunistic species with large forager forces that search independently are more likely to find new resources first. She suggests that environments presenting many small resources and rare, large, high-quality resources of transient availability would select for an independent, opportunistic foraging strategy, rather than recruitment to and defense of resources. This type of resource distribution may well be consistent with that encountered by many social wasp species.

**INTERACTIONS AND ACCESS TO RESOURCES**

Interactions among foragers are important determinants of whether wasps gain and/or retain control of resources in the field (71, 106). The previous section documents the use of visual and olfactory cues in recruitment of foragers. In order to ascertain the roles of particular cues in recruitment, many of these experiments used odors, stationary visual cues, or restrained wasps that could not freely interact with incoming foragers (96, 100, 110, 112). Unrestrained wasps that encounter one another on resources may behave agonistically or tolerantly. The outcomes of these interactions determine which foragers are permitted or denied access to which resources.

**Interactions on Carbohydrate Resources**

Keyel (71), Parrish & Fowler (100), and Parrish (99) observed agonistic interactions among foraging yellowjackets on carbohydrate resources, suggesting that wasps compete for these resources (71). In agonistic interactions, an approaching forager may fly close to a feeding wasp or hover and contact a feeding wasp with her legs, two wasps may hover face to face and fly upward together, or wasps may grapple, which is sometimes accompanied by sting attempts (71, 99). Keyel (71) observed yellowjackets foraging on trees with scale insects producing honey-dew. He artificially enriched these resources by adding basswood honey to randomly selected leaves. Wasps tended to have the lowest percentage of aggressive encounters on natural or highly enriched leaves and had their highest percentage of agonistic interaction on slightly enriched leaves.

Parrish (99), in observations of *Vespula maculifrons* and *V. germanica* foragers of known nest origin, found that interspecific aggression was greater than intraspecific aggression. Within a species, nestmates were not treated preferentially if encountered on a resource. Levels of aggression were related to bait size and persistence—wasps accumulated more quickly on large baits. While the number of wasps increased on a feeder over time, the number of aggressive acts per sample period increased and then decreased at high densities, where the cost of fighting was likely to outweigh any possible benefits. Parrish (99) suggested that
the probability of encountering a nestmate on a resource when it is first available and when wasps are most likely to fight to gain access to the resource is low, and thus foraging yellowjackets should always defend food aggressively in this situation, leading to the unexpected aggression among nestmates at resources.

Interactions on Prey

Raveret Richter (106) experimentally determined the effects of wasp species, nest affiliation, arrival order and prey size on the agonistic behavior of Polybia occidentalis and Polybia diguetana, two species of Neotropical, swarm-founding social wasps. Foragers of both species hovered near pieces of Bagisara repanda (Lepidoptera: Noctuidae) prey occupied by another Polybia forager in preference to unoccupied prey, but their subsequent responses differed. Foragers of P. occidentalis, the larger of the two species, tended to land with other Polybia foragers and gained access to prey by either displacing the resident wasp or splitting the prey with her. In contrast, Polybia diguetana foragers did not land preferentially on occupied prey, and in only 2 out of 50 trials, both when landing with a conspecific, did they successfully displace a resident wasp from her prey.

In intraspecific and interspecific tests, tolerance among wasps varied with prey size. The greatest percentage of highly agonistic activity occurred when a resident wasp was on the largest piece of prey that she had the potential of carrying away; beyond that size, levels of agonistic activity decreased. The overall percentage of agonistic behavior in trials was lower in cases where the larger wasp, P. occidentalis, arrived first at the prey. Nest affiliation did not influence agonistic interactions between foragers; there was no preferential treatment of nestmates by conspecific foragers.

Wasps appeared to behave according to the following rules: If a forager was able to fly off with a piece of prey and thus avoid conflict, she departed with the prey; she fought if she had a chance of excluding others and monopolizing the prey; two foragers would split large prey. The defensibility of the prey and the wasps’ ability to opportunistically take advantage of this defensibility structured the interactions between wasps.

When tracking hunting wasps in the field, Raveret Richter (105, 106) often observed foragers flying toward other wasps standing stationary on vegetation. Large Polistes foragers approaching smaller Polybia would often pounce upon the smaller wasp, and if the smaller Polybia had prey the larger Polistes would take it from her. Smaller wasps approaching larger wasps that had prey often hovered, backed away, and repeatedly re-approached the site until the resident wasp had flown. These observations, combined with the experiments described here and in the previous section, suggest that the presence of other wasps on prey may increase the chance of a forager perceiving or locating the prey. However, one might consider this preferential attentiveness and, when possible, landing and feeding on the prey, as opportunistic theft of prey, rather than facilitation or enhancement of foraging. Theft might even be a foraging tactic employed fac-
ultatively by individual foragers. LJ McPheron (unpublished observation) reports that, in greenhouse studies of *Mischocyttarus flavitaris*, she observed wasps chasing one another at sites where food was presented, and one individual appeared to specialize on taking prey from other wasps rather than hunting for her own prey.

Competition for prey need not require direct interactions among foragers. Rav-eret Richter (105) observed a *Mischocyttarus immarginatus* forager kill a large caterpillar and fly to the nest with a portion of the flesh. While the *M. immarginatus* was at the nest, a *Polistes instabilis* forager landed and took a portion of the prey. The *P. instabilis* left, and *M. immarginatus* returned within three minutes, took a portion of the prey, and flew. While the prey was unoccupied, it was discovered by a *Polybia diguetana* forager who bit off a piece of flesh and flew with it as a *P. occidentalis* forager approached the carcass. This example clearly illustrates how, while prey is left unattended as a forager transports loads to the nest, it can be exploited by other wasps.

**INFLUENCES OF WASP FORAGING ON COMMUNITIES**

**Selective Pressures on Lepidopteran Prey**

Lepidopteran larvae, most of which are specialist herbivores that feed on plants in one or a few genera or in a single family or subfamily (9), are an important prey source for many social wasps (1). In choice tests presenting pairs of caterpillars, one a generalist and one a specialist, to foraging *Mischocyttarus flavitaris*, Bernays (9) found that the generalist caterpillars were preyed upon more readily than were the specialists. Subsequent tests with other generalist predators such as the predatory ant *Paraponera clavata* (26), the Argentine ant *Linepithema humile* Mayr (= *Iridomyrmex humilis*, 116a) (11), and the coccinellid beetle *Hippodamia convergens* (10) also demonstrate preferential selection of generalist caterpillars by these predators. This preference might be partially explained by the association of host-plant specialization by caterpillars with either the sequestration of host plant phytochemicals or the presence of toxic leaf material in the gut of these specialist herbivores (13, 85). Preference by the above-mentioned predators for generalist prey supports the hypothesis that natural enemies such as social wasps provide selective pressures that influence the host-plant specificity of their herbivore prey (9, 26, 118).

Generalist caterpillars tend to have cryptic coloration and behavior (121). Specialist caterpillars, on the other hand, are sometimes warningly colored and unpalatable, and thus aposematic and conspicuous (13). Aposematic caterpillars may be less likely to be attacked by most predators (13), but this is not always the case. Stamp (118) demonstrated that caterpillars of the non-cryptic, specialist buck moth *Junonia coenia* (Lepidoptera: Nymphalidae), which has passive, chemical defenses, were actually more susceptible to predation by wasps (*Polistes*...
fuscatus) and predatory stinkbugs (Podisus maculiventris) than were caterpillars of the cryptic generalist tiger moth Spilosoma congrua (Lepidoptera: Arctiidae), which employs cryptis and rapid fleeing as protection from predators. These invertebrate predators were undeterred by the buck moths' passive, chemical defenses. As they gained experience, however, wasp foragers began to reject the specialist forager, although their rate of predation on the cryptic generalist remained constant (85, 118).

One might expect gregarious, unpalatable caterpillars to be protected from vertebrate predation (22). However, defenses effective against vertebrate predators are not always effective against invertebrates. In field observations on social wasp (Polistes dominulus and P. fuscatus) foragers and gregarious, conspicuous, black and spiny Hemileuca lucina (Saturniidae) larvae, the wasps were undeterred by the urticating spines of the caterpillars, and killed 77% to 99% of the caterpillars at the study site (13, 119). Upon killing the caterpillars by biting, Polistes foragers proceeded to process the caterpillar flesh by biting off the spines, and then transported loads of caterpillar flesh back to their nests (105). Because these wasps tend to return to sites of past hunting success, aggregated caterpillars are particularly vulnerable to depredation by returning foragers.

In the case of Hemileuca lucina caterpillars, attacks by Polistes wasps and other natural enemies not only result directly in caterpillar deaths by predation (119), but indirectly reduce the survival of the caterpillars by inducing alterations in the foraging behavior of the caterpillars. Aggregations of the caterpillars are disrupted (22) and the caterpillars are forced to forage in cooler microhabitats with poorer-quality leaves. This alteration results in poorer larval growth (119) and reduces survivorship. Of the reduction in H. lucina survivorship attributed to the presence of Polistes foragers, one-third was due to these indirect effects (120), which may have their greatest impact upon easy-to-locate, warningly colored caterpillars that are gregarious (13).

Social Wasps as Introduced Species

Humans have inadvertently introduced non-native social wasps into many areas: for example, Vespula germanica is thought to have been accidentally brought to New Zealand during World War II in a crate of airplane parts (124). Vesinae in the Vespula vulgaris species group (wasps having large, long-lived colonies) are the most apparent of these introductions, both because of the sheer abundance of the wasps, and because of their pestiferous interactions with humans (2). Introductions of social wasps with smaller colony size, such as the European paper wasp Polistes dominulus, recently introduced into the Boston vicinity (48), receive lesser notice. However, the ecological impacts of all introduced wasps, including competition with (45) and predation upon (37) native species, also warrant attention.

V. germanica, native to Europe, has become established in many locations outside of its native range (2, 71). Most of these areas had no native yellowjackets
However, in the northeastern United States where it was introduced in the late 1960s (88), V. germanica has become common despite the presence of nine native yellowjackets, three of which are close relatives (71). The establishment of V. germanica under these circumstances may have occurred in part because of its tendency to nest within the walls of houses (71, 88) and in part due to its numerical dominance on rich, human-related food sources (71) to which it recruits by both nest-based, odor-mediated (95) mechanisms, and by field-based mechanisms that include marking of feeding sites with a substance that is attractive to conspecific foragers (Sl. Overmyer & RL. Jeanne, unpublished data) and local enhancement of foraging (71, 100, 110, 112).

Vespula colonies typically are annual and are initiated by a single queen (2). However, in the warmer portions of the wasps’ natural range and in some mild climates where they have been introduced, Vespula may attain enormous colony size by overwintering, enabling the nests and their resident populations to grow much larger than those of the typical annual colonies and leading to an extended foraging season (43). A high incidence of overwintering colonies occurs in Maui, where Vespula pensylvanica became established in 1978. These colonies exert a much greater level of predation pressure on local fauna than the level of pressure expected from smaller annual colonies with shorter seasonal windows of activity (38). In addition, unlike most other invasive species that have colonized the low-elevation coastal regions of the Hawaiian archipelago, V. pensylvanica is best established at high elevations, at sites corresponding with refuges of high endemcity, and the wasps include endemic arthropods as a substantial portion of their diet (37, 38). Small populations of endemic arthropods, having evolved in the absence of vespine predation, may be unable to recover from such perturbations (37).

In New Zealand, where V. germanica was introduced in approximately 1945 (47), these wasps may build huge perennial colonies attached to tree trunks (117). Vespula vulgaris, introduced to New Zealand in the late 1970s, is replacing V. germanica in honeydew beech forest habitats (46, 47). V. vulgaris foragers have great dietary overlap with native insectivorous birds (7, 45). In the honeydew beech forests of the Nelson region on New Zealand’s South Island, the estimated current biomass of V. vulgaris in the community, 5,200 g/ha at the peak of colony growth, is greater than the maximum estimate of the combined biomass of birds, rodents, and stoats, approximately 1150 g/ha (127). In the northern portion of South Island, Harris estimates prey harvest by these wasps at the rate of 8.1 kg/ha during the portion of the year when they are active, an amount similar in magnitude to the approximate yearly consumption by the entire bird fauna in an equivalent area (45). Carbohydrate collection by the wasps, primarily from secretions of the abundant beech scale insect Ultracoelostoma assimile (Homoptera: Margarodidae), is estimated to be at the rate of 343 liters/ha (45), which greatly reduces both the abundance and quality of honeydew available for native wildlife and makes the resource virtually unavailable to birds for three to four months of each year (84). If invertebrate prey or carbohydrate honeydew availability are
limiting resources for native birds, there is clear potential for the wasps to have a negative impact on bird populations (7, 45, 84).

Social Wasps in Biological Control

Virtually all examples of successful pest control using social wasps involve the control of caterpillars. The presence of *Polistes* wasps has been associated with decreased damage from lepidopterous pests of cotton (6, 55, 72), tobacco (75, 104), and cabbage (40, 103). Studies in Brazil on coffee plantations showed that *Polybia occidentalis* and *Brachygaster lecheguana* predation on larvae can be an important factor in checking outbreaks of the coffee leaf miner [*Perileucoptera coffeella* (Lepidoptera: Lyonetiidae; 42, 98)]. Fall webworms [*Hyphantria cunea* (Lepidoptera: Arctiidae; 87, 92)] and gypsy moth larvae [*Lymantria dispar* (Lepidoptera: Lymantriidae; 36)] are also preyed upon by *Polistes* wasps, demonstrating that the wasps are not necessarily thwarted by spines or silk webbing. *Polistes* wasps have also been used in conjunction with pesticides to control crop pests (75). In plots the size of a home garden, *Polistes* foragers have a significant impact on caterpillar populations (40; MA Raveret Richter, personal observation).

Certain features of the feeding biology of social wasps seem especially well-suited to dealing with outbreaks of pest species. The wasps return repeatedly to sites where they have had success in feeding. This behavior would tend to concentrate them disproportionately in areas where there are high caterpillar densities (89). Group-feeding caterpillars may disperse in response to harassment or attacks by wasps (22) and thereby escape wasp predators, suggesting that wasps might be of limited effectiveness in controlling caterpillars with this escape response. However, short-term avoidance of direct predation may come at a cost: If caterpillars escape danger by leaving their host plants or moving to less favorable foraging sites, their growth rate may decrease and larval development time may increase, broadening their window of vulnerability to parasites, predators, diseases, and inclement weather. Stamp & Bowers suggested that such indirect effects on caterpillars may, in addition to the effects of direct predation, contribute to decreases in the populations of pest caterpillars (119).

Wasps have clearly demonstrated promise in providing some degree of biological control of pests under circumstances described here. Unfortunately, the life cycles of the wasps are not always well synchronized with those of sympatric pest Lepidoptera. For example, gypsy moth outbreaks in northeastern North America occur long before social wasps in the area have experienced their seasonal population buildup. In addition, unlike species specific parasitoids, these generalist predators may switch to alternate, more abundant prey when they have decreased the pest population, leaving the target species at higher densities than those required for effective pest control (40).

Methods have been developed for managing colonies of wasps for purposes of biological control (39). However, social wasps vary greatly in their life histories, behavior, and ecology. Many different situation-specific management tech-
niques will need to be developed to fully exploit the biological control potential of these insects to the same degree that, for example, we exploit the behavior of managed colonies of honey bees in crop pollination.

CONCLUSIONS

Water, prey, and carbohydrate availability can limit the productivity of social wasp colonies (53, 113). The studies on which this review focuses demonstrated enormous variability both within and among social wasp species in the mechanisms of foraging for these resources. Although as species social wasps are generalist foragers, at any given time individual foragers may specialize on particular foraging tasks (91), foraging locations (106), and similar to many solitary wasps, on specific prey types (106). Recruitment to resources is poorly developed in these social insects, despite the existence of behavioral mechanisms such as trail pheromones that could be used by swarm-founding social wasps for this purpose. Social wasps associate cues with particular resources, respond to the presence of other foragers on resources, and are influenced by their past foraging experiences. Better understanding of the relationship between environmental conditions and wasp foraging behavior is key to understanding the foraging strategies and tactics of these wasps, including how they use cues to locate and choose resources, and how they respond to changes in resource distribution and abundance. Greenhouse or screen enclosure-based studies of wasps would provide opportunities to follow individual foraging histories and to manipulate resource distribution and abundance under controlled conditions. Such studies could be useful in clarifying behavioral mechanisms of foraging.

Social wasps, by virtue of their behavior and their numbers, can have an enormous impact upon other organisms. Predation by social wasps has both direct and indirect effects on prey (37, 119). A clearer understanding of these effects will prove useful in evaluation of the potential impacts of generalist predators on the evolution of their prey. In addition, an improved understanding of the role of social wasps in communities will have both predictive and possibly ameliorative potential in areas where non-native wasps have been introduced and are having impacts upon the native fauna. Such knowledge may also prove useful in employing the wasps as biocontrol agents in integrative pest management.

Social wasps possess a wide variety of life histories and social systems, which, combined with the varying ecological circumstances in which the wasps occur, present a rich opportunity for comparative studies to illustrate the relationships among social systems, foraging behavior, and the distribution and abundance of resources. Work so far has illustrated many of the possibilities. General patterns, such as the apparent relationship between life history and foraging behavior in the *Vespula vulgaris* and *V. rufa* species groups of yellowjackets (2, 43), have begun to emerge. Even among these vespines, however, additional observation (107, 110) reveals exceptions to past generalizations (2) and predictions (112). Additional data on the mechanisms and patterns of foraging, the variability within...
and among species, and the relationship between environmental parameters and foraging behavior, particularly in less well-known groups such as the Stenogastrinae and the diverse, swarm-founding Polistinae, is necessary in order to distill general patterns and enable a synthetic view of the foraging behavior and ecology of social wasps.

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